TEMPORAL AND SPATIAL ANALYSIS OF KILLER WHALE SIGHTINGS IN THE GALÁPAGOS MARINE RESERVE, ECUADOR

A Thesis

by

KERRI JEAN SMITH

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2012

Major Subject: Marine Biology

Temporal and Spatial Analysis of Killer Whale Sightings

in the Galápagos Marine Reserve, Ecuador

TEMPORAL AND SPATIAL ANALYSIS OF KILLER WHALE SIGHTINGS IN THE GALÁPAGOS MARINE RESERVE, ECUADOR

A Thesis

by

KERRI JEAN SMITH

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Approved by:

Co-Chairs of Committee,	Douglas C. Biggs
	Jane M. Packard
Committee Members,	William E. Grant
	Bernd Würsig
Intercollegiate Faculty Chair,	Gilbert T. Rowe

May 2012

Major Subject: Marine Biology

ABSTRACT

Temporal and Spatial Analysis of Killer Whale Sightings

in the Galápagos Marine Reserve, Ecuador. (May 2012)

Kerri Jean Smith, B.S., Texas A&M University at Galveston

Co-Chairs of Advisory Committee: Dr. Douglas C. Biggs
Dr. Jane M. Packard

A study was conducted using data compiled from two sources to test the hypothesis that killer whales display seasonal variability in their occurrence in the Galápagos Marine Reserve (GMR), Ecuador. Three questions arise from this hypothesis: 1) do killer whale sightings display temporal variability; 2) are sightings spatially associated with resources; and 3) if sightings are spatially associated with resources, does the spatial association change temporally? I combined and evaluated two sets of GMR killer whale sighting data (n=154) spanning a twenty-year time frame collected via opportunistic sightings by an observer network and shipboard line-transect surveys. I tested for a (a) correlation between the total annual sightings and bi-annual seasonality (upwelling versus non-upwelling); (b) correlation between the total annual sightings and the Multivariate El Niño Southern Oscillation Index (MEI); (c) correlation between sightings, the MEI, and seasonality; (d) spatial association between sightings and resources; and (e) spatial change in sightings with seasonality. Sightings were roughly equally distributed between non-upwelling (56%) and upwelling seasons

(July-December). No direct correlation was found between sightings and the MEI. Sightings occurred more often than expected by chance during the peak upwelling months of August-November when the MEI was within one standard deviation of the average (binomial $z=2.91$, $p<0.05$). Sightings were spatially associated with areas of high chlorophyll a values (binomial $z=4.46$, $p<0.05$), pinniped rookeries (binomial $z=6.03$, $p<0.05$), and areas with high combined resource value (binomial $z=5.36$, $p<0.05$). The spatial distribution of sightings did not shift with seasonality, with the exception that sightings occurred less often than expected in areas of low combined resource value during the upwelling period (binomial $z=-3.17$, $p<0.05$). Though variability in observer effort should be considered when evaluating these data, these results do not suggest a strong pattern of seasonal occupancy or that killer whales are responsive to El Niño Southern Oscillation events. Further research is needed to determine if killer whales in the GMR comprise a single resident population, multiple resident and transient populations, or if killer whales observed in the GMR are part of a population inhabiting the eastern tropical Pacific region, which visit the area at various times.

DEDICATION

I dedicate this work to my family; without your love, support and encouragement this would not have been possible. Thank you for always being patient as I excitedly rambled about my latest idea, acting as a sounding board at all hours, and helping me to laugh at myself.

ACKNOWLEDGEMENTS

This thesis is the culmination of the work of numerous individuals; many of whom I will never be able to thank, and all of whom I will never be able to thank enough. To my major advisors, Drs. Douglas Biggs and Jane Packard, thank you for your unending patience, support, guidance, and advice. Dr. Biggs introduced me to the wonder that is the Galápagos Islands, provided me with the tools to better understand oceanographic processes, and helped me hone my critical thinking skills. Dr. Packard, provided a warm, dynamic laboratory environment in which my ideas could grow and flourish. To my committee members, Drs. Bernd Würsig and William Grant, thank you for helping me to shape my ideas and ask the right questions, and for your advice and guidance on this manuscript. Dr. Christopher Marshall, thank you for all of the advice over the years, for providing me with research opportunities as an undergraduate student, and for being available when I needed an ear to bend. To the Department of Oceanography, College of Geosciences, and the Marine Biology Interdisciplinary Program, thank you for providing the funds for travel and research in Ecuador. The Departments of Oceanography and Biology supplied funding in the form of teaching assistantships and the Department of Wildlife and Fisheries provided funding in the form of a research assistantship.

A great thank you is due to Godfrey Merlen, without whom this work would not be possible. His dedication to understanding and protecting the Galápagos Island ecosystem will forever be an inspiration to me and many more. His tireless efforts to gather historical records of killer whale observations and work to build a network of

citizen observers within the Galápagos Islands provided a huge chunk of the killer whale data analyzed in this project. Dr. Daniel Palacios, despite not having any idea who I was, answered my e-mails kindly, thoughtfully, and knowledgably. His work on cetaceans and ecosystem dynamics in the Galápagos Islands helped to lay the groundwork for this project, and he provided the additional killer whale data analyzed in this manuscript. Dr. Juan Jose Alava contributed his data on Galápagos sea lions to this project, in addition to freely sharing his ideas and thoughts. His kind and encouraging words were often just what I needed to help me push through a particularly grueling bit of analyses. I will never be able to thank these three enough for their generous support and wonderful guidance.

To the hundreds of individuals who helped to collect the data used in this analysis, thank you. I may never know your name, or be able to shake your hand, but you were an integral part of this project. Your willingness to share your photos, observations, and knowledge of killer whales in the Galápagos Islands made this research possible.

Julia O'Hern took me under her wing and taught me about being a field biologist, shared ideas and provided invaluable guidance and camaraderie. Olivia Lee, Shannon Finerty, Lacy Madsen, and Tiffany Walker, I can't thank you enough for all of your support in all aspects of my life and this project.

And last but not least, thank you to my family, who stuck by me through the ups and downs of this project and still answered the phone even though they knew it was me

calling. While there are many people who deserve my thanks and who contributed to this work, without your strong support this venture would not have been successful.

NOMENCLATURE

CZCS	Coastal Zone Color Scanner
ENSO	El Niño Southern Oscillation
ETP	Eastern Tropical Pacific
GMR	Galápagos Marine Reserve
MEI	Multivariate ENSO Index
MODIS	Moderate Resolution Imaging Spectroradiometer
MPA	Marine Protected Area
NOAA	National Oceanographic and Atmospheric Association
SeaWiFS	Sea-viewing Wide Field-of-view Sensor

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

INTRODUCTION

In the Galápagos Marine Reserve and surrounding waters (GMR) killer whales (*Orcinus orca*) remain an enigmatic species, with most aspects of their biology unknown (Merlen, 1999). Line-transect surveys of the eastern tropical Pacific (ETP) suggest an estimated population of 8,500 killer whales (Wade and Gerrodette, 1993), but it is unknown how many of these animals might utilize the GMR. Merlen (1999) reports sightings of killer whales within the GMR throughout the year, but the information gap leaves an open question: does a resident population exist or is the area used only for transit or as a stop-over point during long-range movements? The purpose of this study is to examine multi-year killer whale sighting data from the GMR to test the residency hypothesis and provide direction for future research efforts.

The GMR is subject to both annual seasonal changes and multi-decadal cyclic El Niño Southern Oscillation (ENSO) events (Sweet et al, 2007), both of which may impact foraging resources available for killer whales (Ballance et al, 2006). El Niño events bring warm air to the region, which suppresses upwelling and decreases southeast trade wind strength and oceanic mixing, while La Niña events amplify mixing and upwelling with cool air and an increase in southeast trade wind strength (Palacios, 2003). I hypothesize that if resource availability and abundance changes on a temporal scale,

---

This thesis follows the style of *Latin American Journal of Aquatic Mammals*.

killer whales may visit the GMR at various times throughout the year to take advantage of these resource pulses. In Chapter II, I test for a relationship between annual killer whale sightings and environmental temporal variability. If killer whale presence is seasonal, rather than permanent, then I expect to find months with little to no killer whale sightings and a correlation between the strength of an ENSO event and the number of killer whale sightings. To address this hypothesis, I test for (a) a correlation between the total annual killer whale sightings and annual seasons; (b) a correlation between the total annual sightings and the Multivariate ENSO Index (MEI); and (c) an association between sightings, the MEI, and seasonal upwelling.

Observations of foraging killer whales in the GMR provide insight into some of the resources they may be utilizing. Killer whales have been observed within areas of high chlorophyll a productivity, where they are known to harass and possibly predate cetacean assemblages, and have been observed feeding on manta rays, ocean sunfish, sea turtles, and possibly hammerhead sharks (Palacios, 2003; Sorisio, 2006; Alava and Merlen, 2009; Merlen, personal communication, 2010). They have also been observed hunting and predating Galápagos sea lions throughout the archipelago (Merlen, 1999; Merlen, personal communication, 2010; Alava, personal communication, 2011). I hypothesize that if killer whales are feeding in areas of high productivity and on sea lions, then killer whale observations may be more spatially associated with regions where these resources are abundant than in areas where they are less abundant. In Chapter III, I test for a relationship between the spatial distribution of killer whale sightings, high chlorophyll a productivity, and sea lion rookeries.

Chlorophyll a productivity in the GMR is highly dependent upon temporal variability, which may in turn have bottom-up influences on the abundance of important prey resources for killer whales (Trillmich and Limberger, 1985; Smith and Whitehead, 1993; Ballance et al., 2006; Hunt 2006; Karnauskas et al., 2010). I hypothesize that if killer whales are found to be spatially associated with chlorophyll a and sea lion rookeries, and they are present in the GMR for most of the year, then they may alter their spatial distribution in response to temporal variability of these resources. In Chapter IV, I address this hypothesis by testing for a shift in killer whale sighting spatial distribution with respect to seasonality.

The ultimate goal of this work is to publish baseline values on killer whale sighting temporal and spatial distribution in the Galápagos Marine Reserve. To accomplish this goal I will aim to publish three chapters from this thesis. Chapters II and III will answer basic questions about the temporal and spatial distribution of killer whales sightings within the GMR, and will be submitted for publication to the *Latin American Journal of Aquatic Mammals*. Building on the results of the tests conducted in Chapters II and III, Chapter IV combines and expands upon the temporal and spatial tests to gain a further understanding of how killer whale sightings are spatially distributed within the GMR in response to temporal fluctuation. Chapter IV will be submitted for publication in *PLoS One*. Both the *Latin American Journal of Aquatic Mammals* and *PLoS One* are free access journals that will make the results of this study readily and freely available to international scientists. In Chapter V, a summary of my thesis research and some recommendations for future research are provided.

CHAPTER II

TEMPORAL ANALYSIS

Introduction

Killer whale sightings in the Galápagos Marine Reserve and surrounding waters (GMR) have been reported since 1948, yet little is known about their residency in this region (Merlin, 1999). Analyzing opportunistically collected data, Merlen (1999) reported sightings of killer whales within the GMR throughout the year. Wade and Gerrodette (1993) estimated a population of 8,500 killer whales in the Eastern Tropical Pacific (ETP), but it is unknown if killer whales observed in the GMR are part of this population. This information gap leaves an open question: does a resident population exist or is the area used as stop-over point during long-range movements?

Killer whale populations are known to make short- and long-range movements of various distances, from hundreds to thousands of kilometers (Hauser et al, 2007; Krahn, et al, 2007; Andrews et al, 2008; Dahlheim, et al, 2008; Foote et al, 2010; Matthews et al, 2011). A recent study by Durban and Pitman (2011) indicates that at least one ecotype undertakes long-distance migrations. In other locations killer whales are known to move between resources on a seasonal basis and take advantage of increased prey availability during resource pulses (Foote et al, 2010; Reisinger et al, 2011).

Seasonal resource abundance varies greatly between southern hemisphere ecosystems, with strong seasonal shifts occurring near the pole and weaker shifts occurring near the equator. In the frigid Antarctica and sub-arctic waters, where

nutrients are plentiful, the sun acts as the driving force in productivity (Sewell and Jury, 2011; Teschke et al, 2011). The extreme shift from a 24 hour photo-period to a 24-hour sun-absent period between seasons results in short-growing high-amplitude phytoplankton and zooplankton blooms in the austral spring and summer (Sewell and Jury, 2011; Teschke et al, 2011). During the austral autumn the resting stages for these blooms lie dormant and primary productivity drastically decreases (Sewell and Jury, 2011; Teschke et al, 2011). In the tropics and sub-tropics nutrients are scarce and the photic period is long and consistent throughout the year, resulting in long-growing low-amplitude blooms (Racault et al, 2012). In pelagic ecosystems productivity can be very low due to low nutrient levels, whereas tropical coastal regions are more productive due to upwelling and increased nutrient levels (Racault et al, 2012). The GMR is unusual among tropical pelagic regions in that it has higher than average primary productivity (Palacios, 2003; Schaeffer et al., 2008) which may make it an ideal foraging resource for killer whales undertaking long-distance movements or migrations, or when seasonal resource abundance decreases in other areas.

Strong El Niño events suppress upwelling, a driving force behind the high primary productivity of the GMR (Sweet et al., 2007; Schaeffer et al., 2008), which may in turn decrease the amount of resources available for killer whales. Strong El Niños have been shown to have a lasting effect on the community structure in the GMR, as evidenced by the 1982-1983 El Niño event that resulted in 100% mortality for Galápagos sea lion pups born in 1982 and an 89% reduction in the number of pups born the following year (Alava and Salazar, 2006). Killer whales may respond to these

fluctuations in potential prey availability by leaving the GMR following these events. Changes to the cetacean community structure as a result of ENSO events have been reported in several locations (e.g. Monterey Bay, California; the Gulf of California; Magdalena Bay, Mexico; Bahia de la Paz, Mexico) and may affect the habitat use and community structure of cetaceans in the GMR (Flores-Ramirez et al, 1996; Gardner and Chavez-Rosales, 2000; Benson et al, 2002; Salvadeo et al, 2011). If resource availability and abundance changes on a temporal scale, killer whales may visit the GMR at various times throughout the year to take advantage of these resource pulses and vacate the GMR when strong ENSO events severely depress resource availability.

The aim of this chapter is to provide new information about the seasonal and inter-annual occurrence of killer whale sightings within the GMR with regard to annual seasonal changes and cyclic El Niño Southern Oscillation events. To achieve this, I analyzed data involving temporal distribution collected via opportunistic sightings by an observer network and shipboard line-transect surveys over a 20 year time frame.

Methods

Data collection and reduction

Killer whale sightings analyzed in this study were collected between the geographic coordinates 94°W and 87°W, 3°N and 3°S (Figure 1). Sightings collected via the observer network were collected opportunistically and with variable effort between 1948 and 1997 by Galápagos National Park tour guides, boat captains, scientists, and film makers (Merlen, 1999). Sightings collected via line transect were collected between 1976 and 2000 on the Ocean Alliance vessels *Odyssey* and *Siben* and NOAA South West Fisheries Science Center research and tuna vessels (Palacios, personal communication 2010). A total of 175 sightings were available for analysis, but only data collected between 1976 and 1997 were analyzed (n = 154). For years 1977 and 1984 no data were available and thus were treated as missing data. This 22 year time frame was chosen because both collection methods were being employed and no more than one year passed without killer whale sightings.

Data analysis

To assess whether any changes in the seasonal or interannual occurrence of killer whales were related to environmental variability, two variables were considered: (1) seasonal upwelling and productivity; (2) the Multivariate ENSO Index (MEI) available from the NOAA Earth System Research Laboratory (ESRL, 2011). I tested for (a) a relationship between annual sighting abundance and seasonal upwelling (b) a correlation between the total annual killer whale sightings and the MEI, (c) a correlation between

the total annual killer whale sightings and the MEI of the previous year, and (d) an association between killer whale sightings, the ENSO index, and seasonal upwelling.

Upwelling was initially defined as a six month period of increased chlorophyll a which consisted of months July – December. Within these six months, July and December may act as transitional months that bound the "peak" upwelling period lasting three to four months and occurring August – November (Sweet et al., 2007; Schaeffer et al., 2008). After excluding the transitional months of July and December, I used a binomial z test (Bakeman and Gottman, 1986) to measure the association between killer whale sightings, the ENSO index, and seasonal upwelling with two three-month variations of this peak, August – October and September – November, and a four month peak of August – November.

I assigned a MEI value to each year of analysis according to the NOAA MEI bimonthly values (Table 1). Each year was classified as either "normal," "El Niño," or "La Niña." Normal conditions were defined as less than one standard deviation from the norm (0); El Niño conditions were defined as at least one positive standard deviation from the norm (1, 2, or 3); La Niña conditions were defined as at least one negative standard deviation from the norm (-1, -2, or -3) (Table 2). If at least one month of the year exhibited a non-normal condition, the year was classified as non-normal. If a year exhibited both El Niño and La Niña conditions, the year was classified according to the more prominent condition, determined by the total number of months each condition was present. The strength of the deviation for the year was assigned according to the strongest deviation present that year.

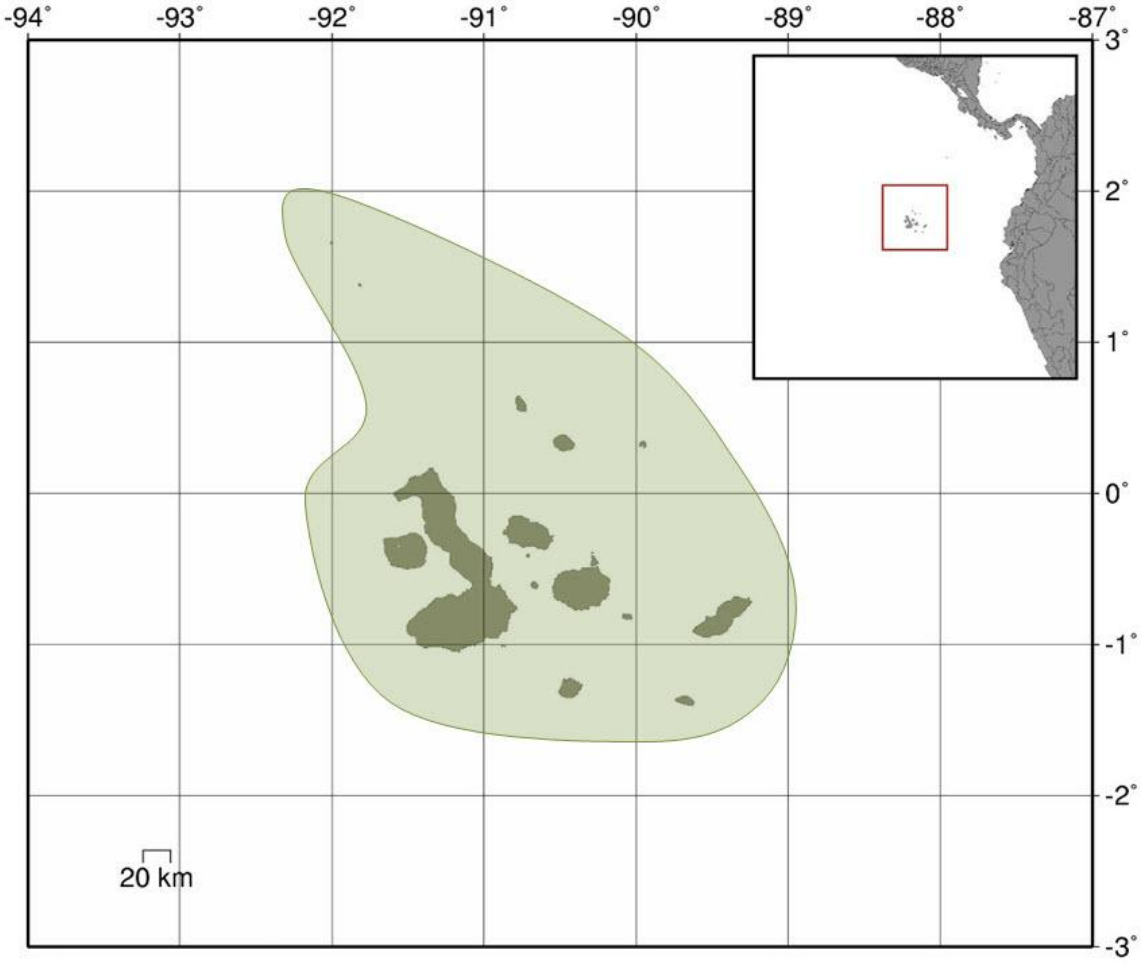

Figure 1: The study area: the Galápagos Marine Reserve, shaded, and surrounding waters. Map created with SEATURTLE.org/Maptool.

Table 1: A summary of the number of sightings and the Multivariate El Niño Southern Oscillation Index condition each year of the study period.

YEAR	NUMBER OF SIGHTINGS	MULTIVARIATE EL NIÑO SOUTHERN OSCLLATION EVENT INDEX VALUE
1976	5	-1
1978	8	0
1979	1	1
1980	8	0
1981	15	0
1982	7	2
1983	3	3
1985	3	0
1986	5	1
1987	2	2
1988	6	-1
1989	10	-1
1990	1	0
1991	5	1
1992	5	2
1993	24	1
1994	13	1
1995	12	1
1996	18	0
1997	3	2

Table 2: A summary of the Multivariate El Niño Southern Oscillation Index value for each El Niño Southern Oscillation condition.

EL NIÑO SOUTHERN OSCILLATION CONDITION	MULTIVARIATE EL NIÑO SOUTHERN OSCILLATION EVENT INDEX VALUE(S)
Normal	0
El Niño	1, 2, or 3
La Niña	-1, -2 , or -3

Results

Killer whale sightings were recorded for every month, though not every month of every year (Figure 2). Sightings were roughly equally distributed between upwelling (44%) and non-upwelling periods (56%), when the non-upwelling period was defined as January – June and the upwelling period was defined as July – December (Figure 3). No relationship was found between the strength of an ENSO event and the number of sightings that year ($r^2 = 0.039$) (Figure 4), and no relationship was found between the strength of an ENSO event and the number of killer whale sightings the following year ($r^2 = 0.118$) (Figure 5). Killer whales were sighted more often than expected during the three-month upwelling peak of August – October and the four month upwelling peak of August – November when the MEI was within one standard deviation of the norm (binomial z score = 2.04, $p<0.05$ and binomial z score = 2.91, $p <0.05$, respectively) (Table 3).

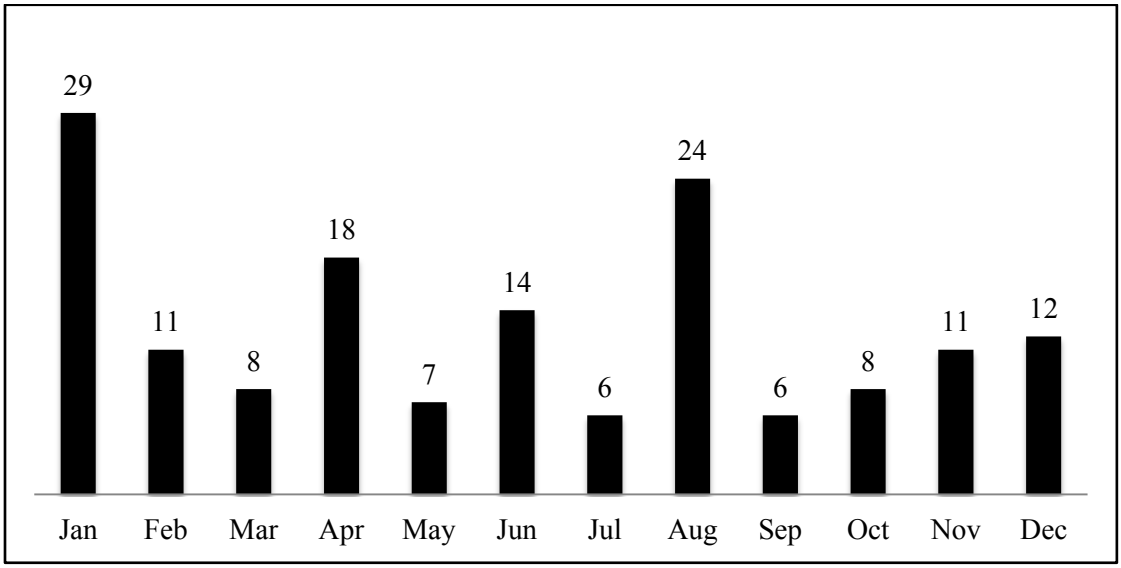

Figure 2: Monthly distribution of killer whale sightings for the study period.

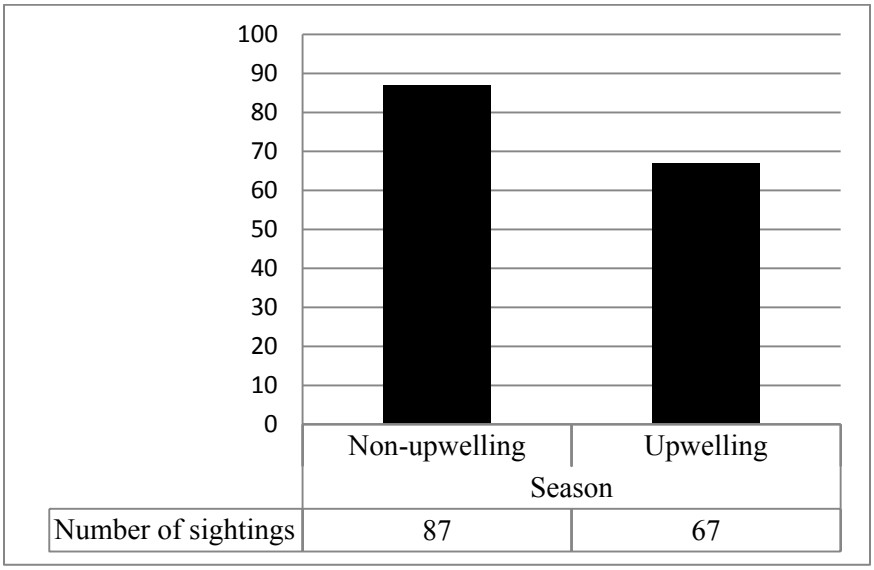

Figure 3: Seasonal distribution of killer whale sightings for the study period. Here the upwelling period includes the transitional months of July and December.

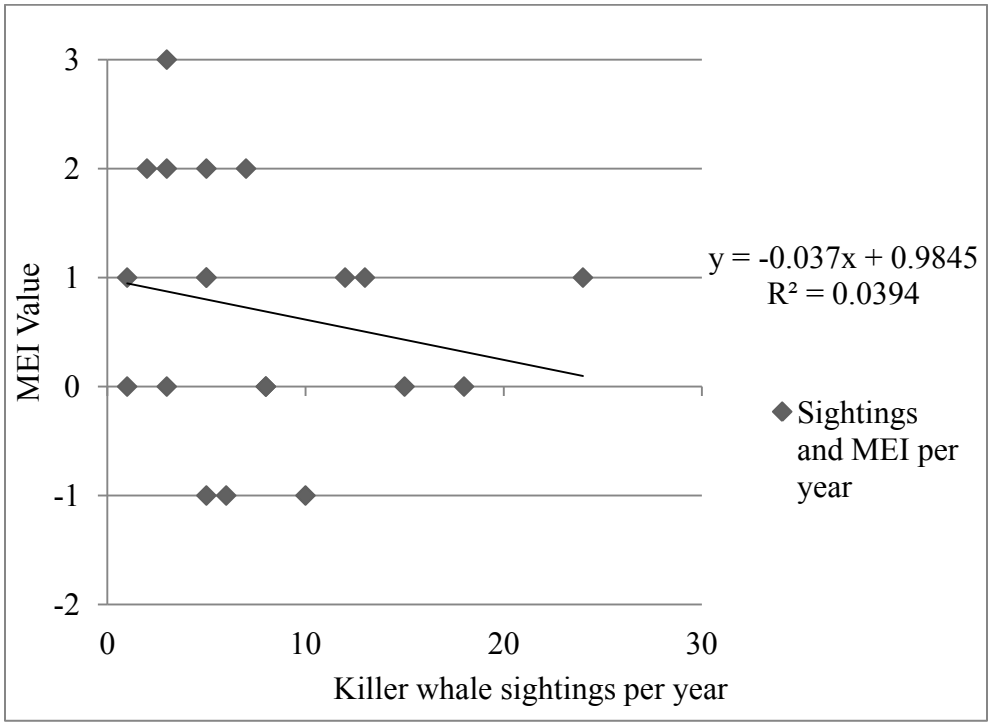

Figure 4: Number of killer whale sightings and the Multivariate El Niño Southern Oscillation Index for each year.

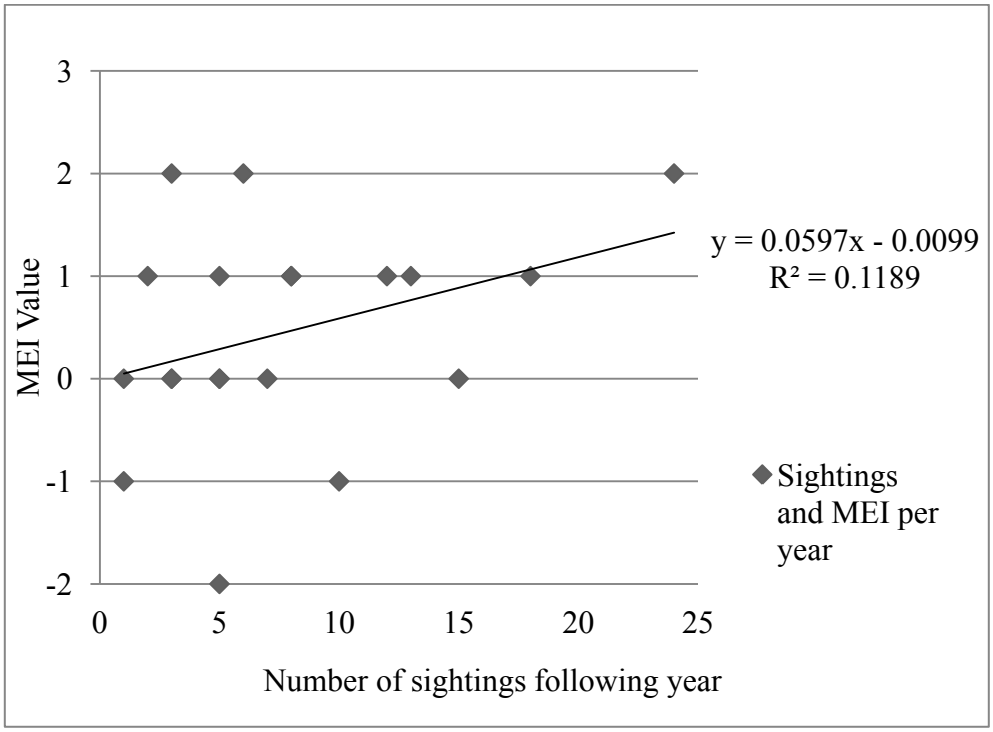

Figure 5: Multivariate El Niño Southern Oscillation Index for each year and number of killer whale sightings the following year.

Table 3: Test results for the strength of association between sightings and upwelling season, based on three definitions of the upwelling peak when the Multivariate El Niño Southern Oscillation Index was within one standard deviation of the average.

UPWELLING PEAK	BINOMIAL Z SCORE	P-VALUE
August - October	2.04	< 0.05
September - November	0.26	> 0.05
August - November	2.91	< 0.05

Discussion

This study represents the first time that multiple reports of killer whale sightings in the GMR have been synthesized and analyzed for temporal patterns. With the caveat that the data collection efforts were not consistent across the collection period, these results provide new insights into the temporal patterns of killer whale sightings in the GMR.

These results support the hypothesis of a continuous killer whale presence in the GMR from month to month and most years. The two years (1977 and 1984) with missing data could be a result of: a) no line-transect surveys conducted those years, b) no observations recorded or reported by opportunistic observers, or c) low killer whale presence due to fluctuating environmental factors. Though I found no association between the strength of an ENSO event and the number of killer whales observed in the following year, no killer whales were observed in 1984, directly following the only El Niño event with a standard deviation of 3 within the study period. Trillmich and Limberger (1985) and Alava and Salazar (2006) report that extreme El Niño events, such as the very strong one that occurred in 1983, have devastating effects on pinniped populations within the GMR, Vargas et al. (2007) demonstrated that the 1983 El Niño event had a catastrophic effect on the population of Galápagos penguins (*Spheniscus mendicus*), and Edgar et al (2010) suggests that the GMR underwent severe transformation at the autotrophic level following the 1983 El Niño. Strong El Niño events suppress upwelling, a driving force behind the high productivity of the GMR

(Sweet et al., 2007; Schaeffer et al., 2008), which may in turn decrease the amount of potential prey resources available for killer whales.

That killer whales were sighted more often than expected during the previously defined peak upwelling periods (August – October, and August – November) when the MEI was normal, may be an indicator of the number of observers present rather than a greater abundance of killer whales. If resources are more abundant during these times there may be more people on the water to take advantage of those resources, and thus more reports of killer whales. This is not to say that killer whales are not more abundant during these periods, but that the interpretation of these results needs to take that possibility into consideration.

Further research needs to be conducted to determine if the same individuals are observed repeatedly or if multiple groups of killer whales are using the GMR throughout the year. Photo identification projects have proven successful for identifying individual killer whales, social groups and residency in other populations, such as Alaska, the Eastern Tropical Pacific, and along the Northwest Pacific coast of North America (e. g. Dahlheim, 1997; Olson and Gerrodette, 2008, Durban et al, 2010). A similar photo identification project in the GMR could prove very valuable in identifying residency patterns of killer whales. Durban and Pitman (2011) and Matthews et al. (2011) both report the success of placing satellite tags on killer whales to gain valuable new insight into their long distance movements. Placing satellite tags on killer whales in the GMR could be a valuable tool to learn more about their movement and habitat use, and if GMR killer whales are migrants from other regions.

These results do not suggest a strong pattern of seasonal occupancy and provide sufficient evidence to reject the hypothesis that killer whales observed in the GMR are present during specific times to take advantage of resource pulses. They do support an alternative pattern, such as a single resident population, multiple resident and transient populations, or that killer whales observed in the GMR are part of a population inhabiting the eastern tropical Pacific region that visit the GMR throughout the year. To better understand what role, if any, seasonality and ENSO events have on killer whales in the GMR additional research needs to be conducted on the spatial distribution of sightings. Merlen (1999) and Palacios (2003) report that GMR killer whales have been observed predating sea lions, possibly predating cetaceans, and foraging in areas of high chlorophyll a productivity. As Chapter III will show, statistical analysis of the spatial distribution of GMR killer whale sightings may help to identify key habitats and resources.

CHAPTER III

SPATIAL ANALYSIS

Introduction

Though some coastal killer whale populations have been extensively studied and are well understood (i. e. the resident ecotype of northwest North America), only a handful of island killer whale populations have been studied. In the southern hemisphere killer whales have been studied around the Prince Edward Islands (PEI) and the Crozet Islands. At the PEI killer whales are observed feeding on fur seals (*Arctocephalus tropicalis*), elephant seals (*Mirounga leonine*) and several species of penguins, (Reisinger et al, 2011). PEI killer whales are present all year with peaks in abundance occurring twice a year, coinciding with an increase in the abundance of penguins and pinnipeds (Reisinger et al, 2011). At the Crozet Islands, located at similar latitude as the PEI, killer whales are observed feeding on fish, penguins, and elephant seals using multiple different foraging tactics. These include patrolling the mouth of rivers where pinniped pups swim, in areas with dense algae cover along penguin colonies, and occasionally predating large cetaceans (Guinet, 1992; Guinet et al, 2000). Like the killer whales at the PEIs, these killer whales are also present all year with occasional abundance peaks that coincide with an increase in prey abundance (Guinet, 1992; Guinet et al, 2000).

In the northern hemisphere, killer whales have been studied in the Aleutian Islands and Hawaii. Killer whales observed in the Aleutian Islands are part of the

transient ecotype known to predate a wide variety of marine mammals, including several species of pinnipeds, river and sea otters, and other cetaceans (Dahlheim et al, 2008; Durban et al, 2010; Matkin et al, 2007). These killer whales are known to travel long distances in order to take advantage of increases in resource abundance and distribution; a recent study by Barrett-Lennard et al (2011) demonstrated that 150+ killer whale annually aggregate around Unimak Island to predate migrating gray whales, often feeding for several days on the submerged carcasses of their prey. In the Hawaiian Islands, a tropical island ecosystem similar the Galápagos Islands, killer whales are infrequently observed yet are known to be present in the region at least nine months of the year (Baird et al, 2006). They are thought to be generalist predators and have been observed predating both cephalopods and humpback whales (Baird et al, 2006).

Killer whales are observed in the Galápagos Marine Reserve and surrounding waters throughout the year, though very little is known about how they are distributed throughout the region or their habitat use (Merlen, 1999; Chapter II). In the GMR, killer whales have been observed near every major island and have been recorded foraging on a diverse array of prey, including cetaceans, sea lions, sharks and rays, fish, and sea turtles (Merlen, 1999; Palacios, 2003; Merlen and Alava, 2009). Merlen (1999) reports that of 135 sightings, 45 (40%) occurred near sea lion rookeries, and Palacios (2003) found that killer whales attacked cetaceans along upwelling zones where levels of chlorophyll a are high. Despite these observations and reports, it is still unknown if sightings are spatially associated with these resources and how killer whales are moving throughout the region.

Seasonal upwelling in the GMR is the driving force behind increased primary productivity and standing crops of chlorophyll a, which in turn are responsible for the high abundance and biodiversity of resources in the region (Sweet et al, 2007; Schaeffer et al, 2008). Because primary productivity provides bottom-up forcing for the GMR ecosystem, increased standing crops of chlorophyll a should lead to increased standing crops of the mid-trophic level resources that killer whales predate (e. g. fish, squid, and baleen whales) (Hunt 2006; Alava, 2009). While distribution and abundance data for many of these mid-trophic level resources are scarce, remotely sensed chlorophyll a data are readily available and can serve as a proxy to indicate areas where mid-trophic levels resources may be located.

Pinnipeds are highly mobile upper trophic level predators that constitute an important role in the diet of several killer whale populations (e.g.: the transient ecotypes of western North America; Crozet Islands; Marion Islands, and Punta Norte, Argentina) (Lopez and Lopez, 1985; Guinet, 1992; Hoelzel, 1991; Ford et al, 1998; and Pistorius et al, 2002). In the GMR there are two resident pinniped species, the Galápagos sea lion and the Galápagos fur seal, both of which killer whales have been observed predating. However, only one known attack has occurred on fur seals, and sea lions are more populous and widely distributed. The majority of sea lion rookeries are found near the center of the archipelago but they frequently travel to other islands or are encountered at sea, while fur seal colonies are predominantly located on Isabela and Fernandina Islands along the outer western edge of the archipelago, and they rarely travel to other islands (Jeglinski et al, 2011; personal observation). Jeglinski et al (2011) found that fur seals

and sea lions overlap in their distribution along the western islands and fur seals and juvenile sea lions both feed primarily at night, while adult sea lions feed both night and day. Merlen (2000) also found that fur seals were more active acoustically at night than during the day. Due to the size discrepancy in adult sea lions and fur seals/juvenile sea lions, nocturnal foraging may be an anti-predator strategy by these smaller animals to avoid predation. However, Jeglinski (personal communication 2011) found that killer whale presence elicited no visual response from fur seals who were in the water when killer whales passed by, suggesting that fur seals may not be frequently predated by killer whales.

Due to the availability of data, this study will focus on the abundance and distribution of two potential resources: chlorophyll a concentrations as a proxy for primary productivity, and sea lion rookeries; and the overlap between these resources. The aim of this chapter is to provide new information about the spatial distribution and resource associations of killer whales within the GMR. To achieve this, I analyzed killer whale spatial sighting data collected via opportunistic sightings by an observer network and shipboard line-transect surveys over a 20 year time frame.

Methods

Data collection and reduction

Data collection and reduction methods for this study are the same as those described in Chapter II. Refer to the Chapter II Methods section for a full description of the methods used to collect and reduce the data set.

Data analysis

To assess whether killer whale sightings were spatially associated with resource abundance, I tested for a relationship between each killer whale sighting and the a) distance to the nearest sea lion rookery in kilometers (Vulnerable Prey Index), b) chlorophyll a concentrations (Productivity Index), and c) combination of distance to sea lion rookery and chlorophyll a level (Combined Resource Availability Index). I accessed chlorophyll a data through the Giovanni online data system, developed and maintained by the NASA Goddard Earth Sciences Data and Information Services Center, and created a chlorophyll a composition map comprised of MODIS 4km resolution satellite data from January 2003 to December 2010 (GES-DISC, 2011). Because remotely sensed chlorophyll a data are unavailable within the GMR except for a brief period during the CZCS mission of 1978-1986 and not again until the launch of SeaWiFS in 1997, I used the current mission of ocean color (MODIS) satellite data (8 years, 2003-2010) to create a map of average chlorophyll a concentrations that incorporates interannual fluctuations from El Niño and La Niña events. I used ArcGIS to map the killer whale sighting and sea lion rookery data on the chlorophyll a composite map, and used a free source random

sample generator script to create 154 random points (ESRI, 2011). I measured the level of chlorophyll a at both the random points and sightings, and used the ArcGIS measuring tool to measure the distance in kilometers from both sightings and random points to the nearest sea lion rookery.

Sightings (Figure 6) and random points (Figure 7) were assigned to a Productivity Index value according to the chlorophyll a concentration at the location of the sighting or point (Figure 8, Table 4). Each sighting and random point was also assigned a Vulnerable Prey Index value according to the distance in kilometers from the sighting or point to the nearest sea lion rookery (Figure 9, Table 4). I tested multiple variations of the association between data points and sea lion rookeries, including using a five-tier measuring system (instead of the three-tier used in this analysis), categorizing sightings as <5km, 5-10km, and >10km, and categorizing sightings as <10km, 10-30 km, and >30km. In each case the results were primarily the same: the category(ies) nearest the rookeries had more sightings than expected by chance; the category(ies) farther from rookeries had less sightings than expected by chance; and the mid-distance category(ies) either had more sightings than expected or they did not differ from the expected value, but in no cases did they have less sightings than expected by chance. Because the results did not change due to the category system employed, to simplify the presentation of results I chose to use the three-tier system described in the methods section rather than an alternate category system.

Each sighting and random point was then assigned a Combined Resource Availability Index value based on the Productivity and Vulnerable Prey Index values (Table 4). For a sighting or point to be labeled "high," it needed to be located < 20km from a rookery and within ≥ 1mg/m^3 chlorophyll a. To be labeled "moderate" it could be any of the following combinations: chlorophyll a ≥ 1mg/m^3 and distance 20-49.99km; chlorophyll a 0.3-0.99 mg/m^3 and distance 20-49.99km; chlorophyll a 0.3-0.99mg/m^3 and distance <20km; chlorophyll a ≥ 1mg/m^3 and distance ≥50km; chlorophyll a <0.3mg/m^3 and distance <20km . To be labeled "low" it could be any of the following combinations: chlorophyll a <0.3 mg/m^3 and distance 20-49.99km; chlorophyll a 0.3-0.99 mg/m^3 and distance ≥50 km; or chlorophyll a <0.3mg/m^3 and distance ≥50km. I used a binomial z test (Bakeman and Gottman, 1986) to compare the probability of co-occurrence of killer whale sightings with the number of randomly generated points for each resource category.

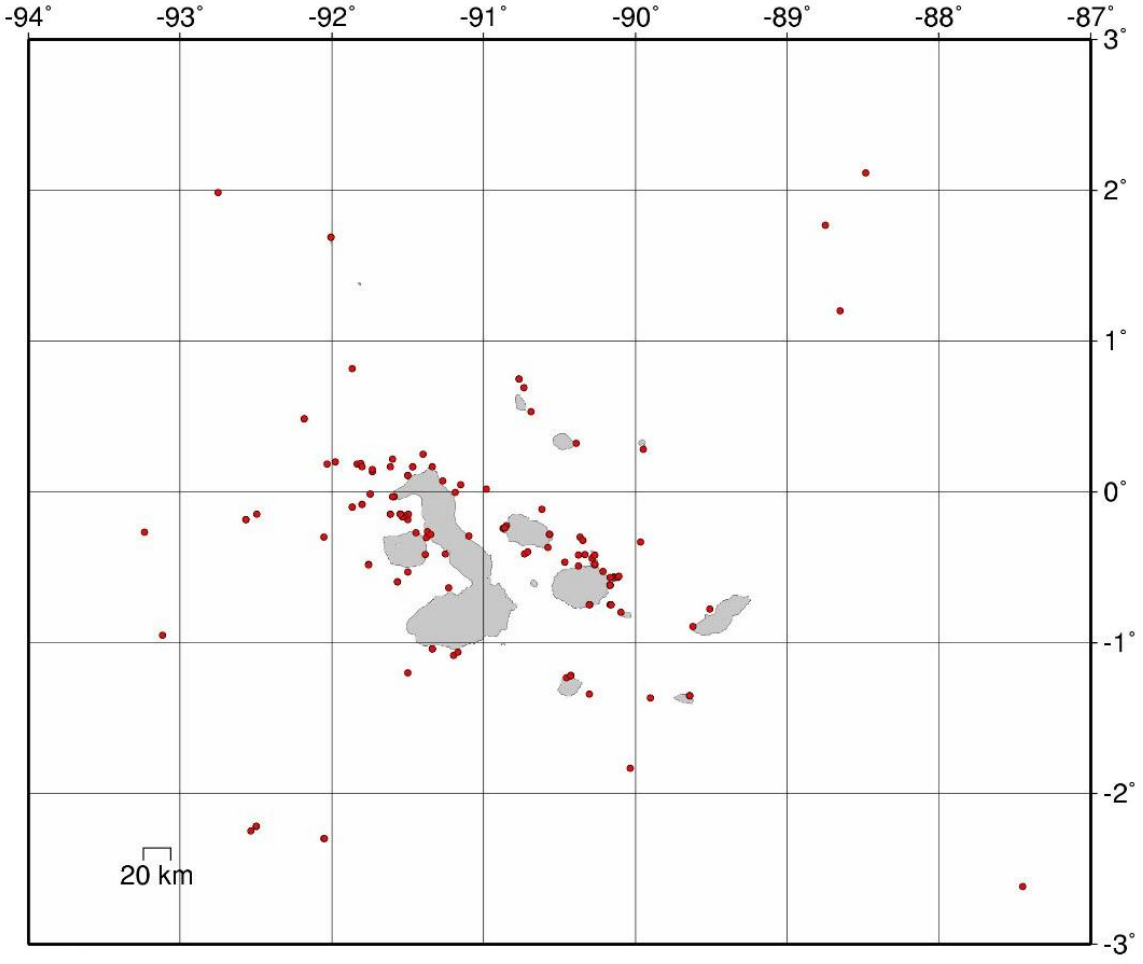

Figure 6: Spatial map of killer whale sightings (1976-1997), combining results of opportunistic and systematic surveys. Some dots represent more than one sighting.

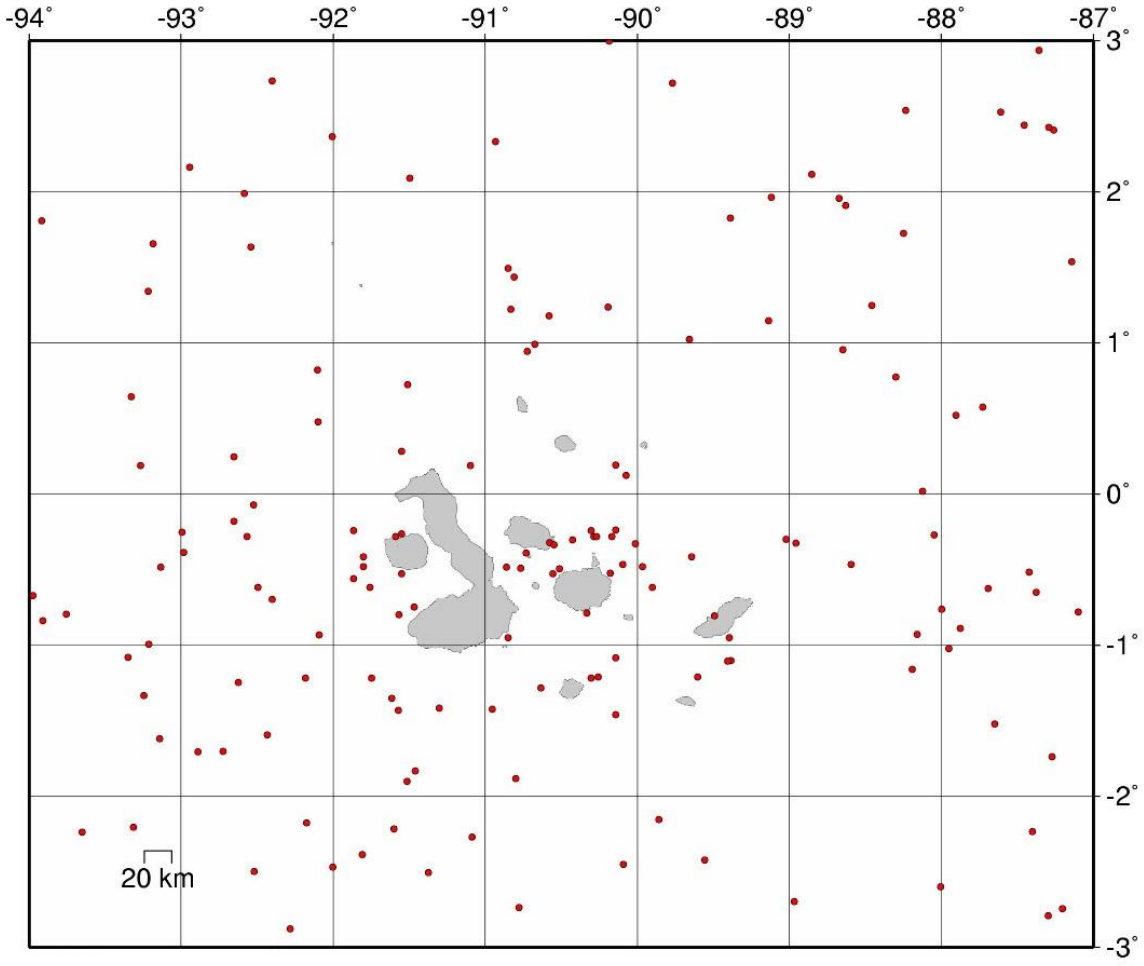

Figure 7: Spatial map of randomly generated data points used for comparison of available and observed habitat conditions associated with killer whale sightings.

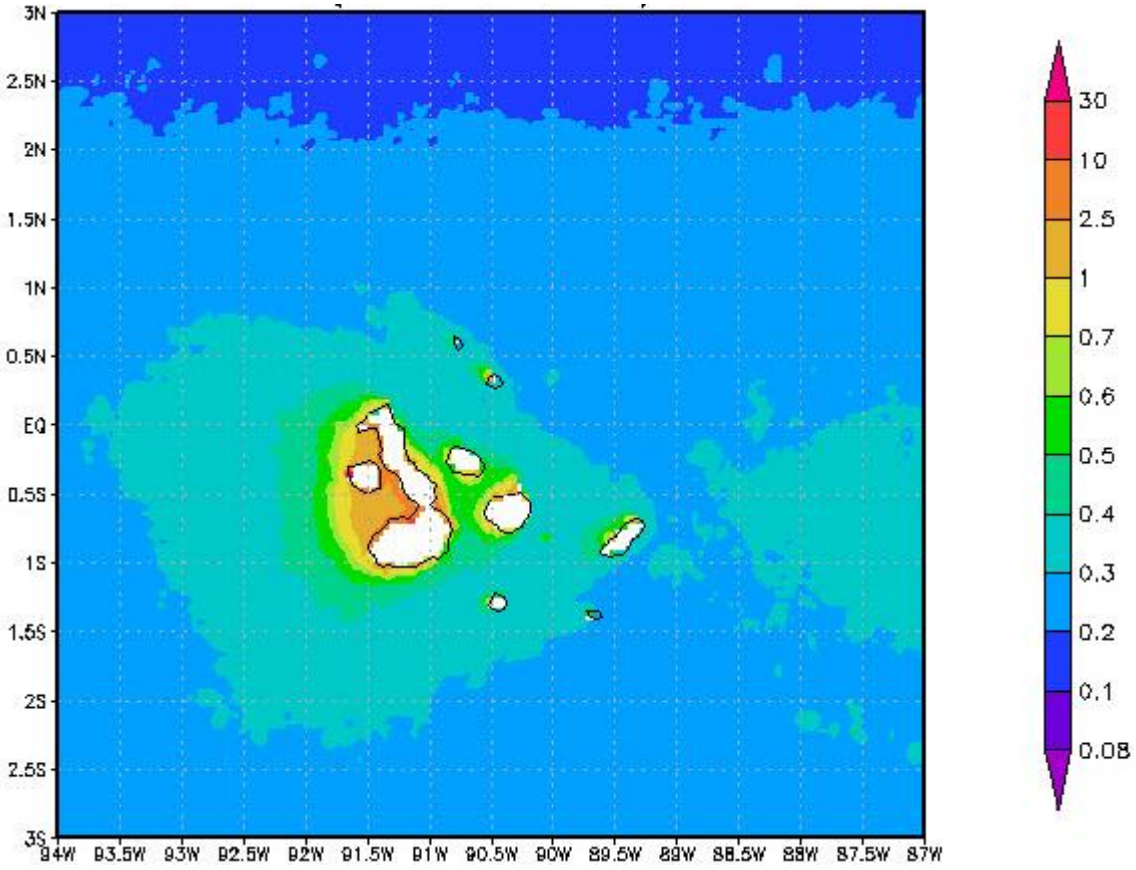

Figure 8: Composite chlorophyll a map generated from MODIS satellite data for the period January 2003 – December 2010. Resolution is 4km and chlorophyll a values are measured as mg/m^3.

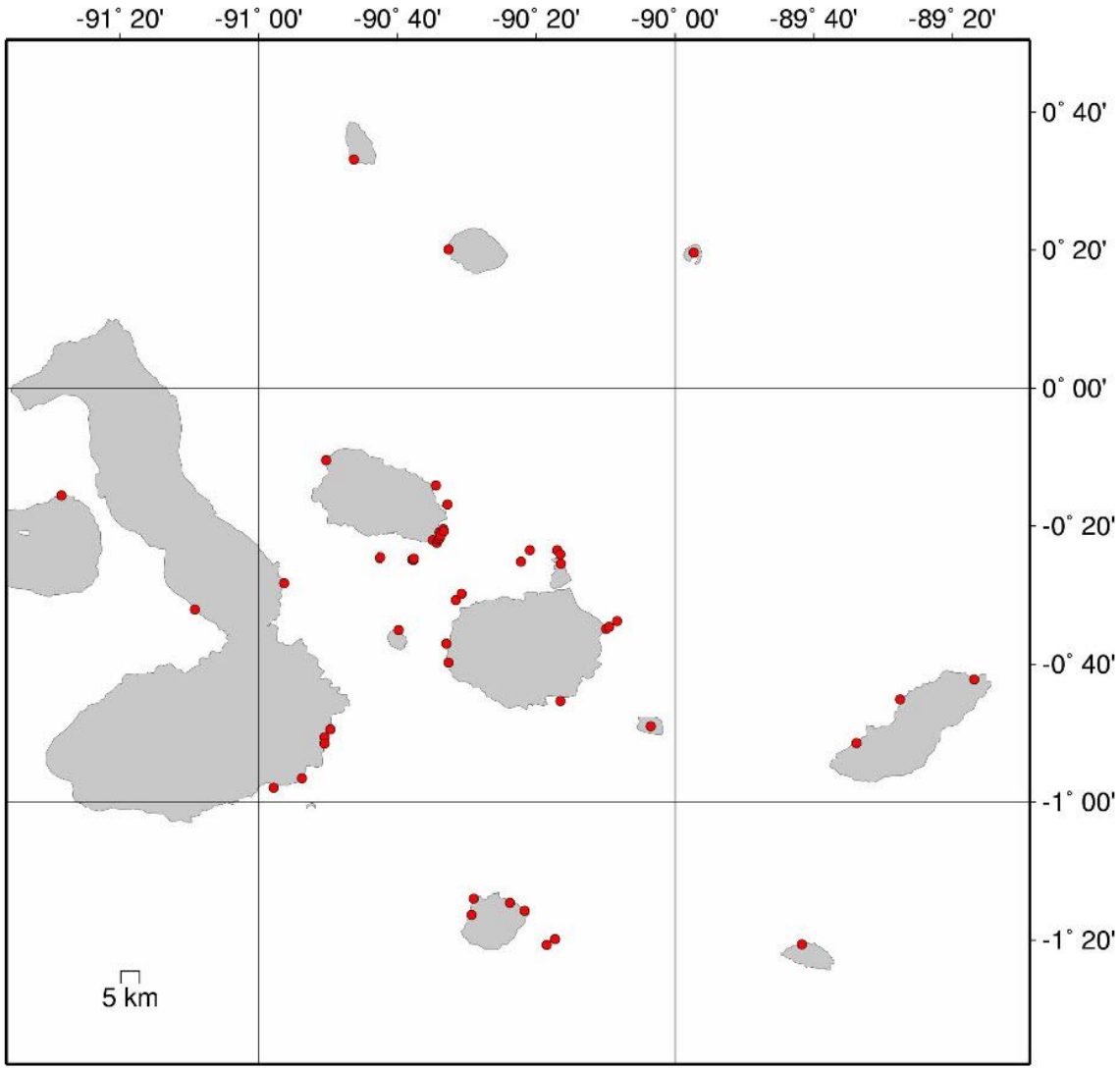

Figure 9: Sea lion rookery and haul out locations in the Galápagos Marine Reserve. Adapted from Alava and Salazar (2006) and Fariña et al (2003).

Table 4: Indices for Productivity, Vulnerable Prey, and Combined Resource Availability.

PRODUCTIVITY INDEX (MG/M^3)	VULNERABLE PREY INDEX (DISTANCE IN KM)	COMBINED RESOURCE AVAILABILITY INDEX
Low (< 0.3)	Low (≥50)	Low
Moderate (0.3–0.99)	Moderate (20–49.99)	Moderate
High (≥ 1)	High (< 20)	High

Results

When sightings were tested for an association with the Productivity Index against the randomly generated points ("chance"), sightings were observed more often than expected with the Index values of high (binomial $z = 4.46$, $p<0.05$) and moderate (binomial $z = 2.61$, $p<0.05$). Sightings were observed less often than expected by chance with an Index value of low (binomial $z = -5.88$, $p<0.05$) (Figure 10, Table 5).

When tested for an association with the Vulnerable Prey Index, sightings were observed more often than expected by chance with the Index value of high (binomial $z = 6.03.$, $p<0.05$). When the Index value was moderate sightings were not found more or less often than by chance (binomial $z = 1.47$, $p>0.05$). Sightings were found less often than expected by chance with the Index value of low (binomial $z = -5.90$, $p<0.05$) (Figure 11, Table 5).

When tested for an association with combined resource availability, sightings were observed more often than expected by chance when availability was high (binomial $z = 3.64.$, $p<0.05$) and moderate (binomial $z = 5.87$, $p<0.05$). Sightings were found less often than expected by chance when the availability was low (binomial $z = -6.62$, $p<0.05$) (Figure 12, Table 5).

The spatial mapping of the sightings indicated two areas that may be of higher use by GMR killer whales: northwest Isabela Island and the head of the Bolivar Canal; and Seymour Norte/Baltra/northeast Santa Cruz (Figure 13).

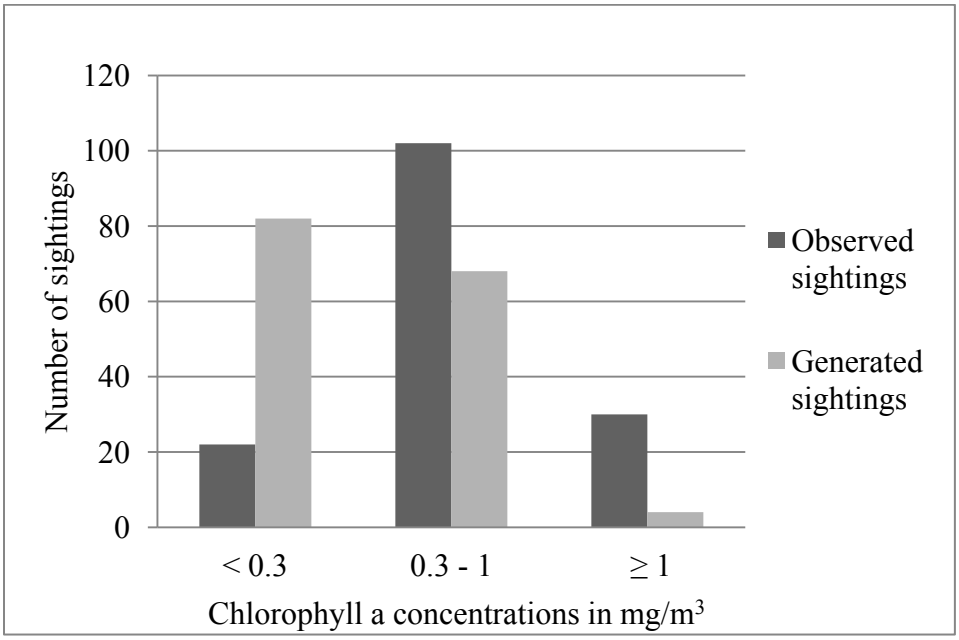

Figure 10: Association of observed sightings with three categories of the Productivity Index, compared to randomly generated sightings.

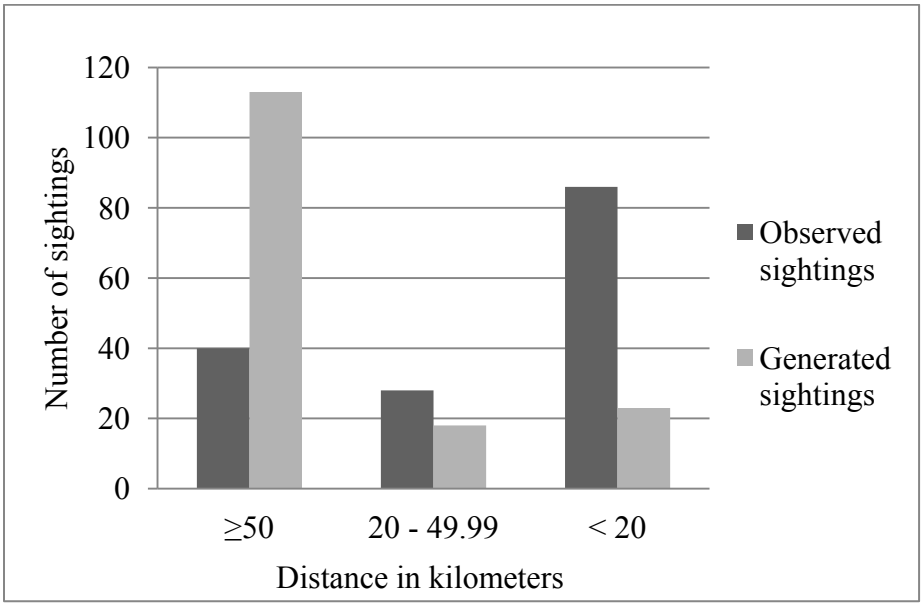

Figure 11: Association of observed sightings with three categories of the Vulnerable Prey Index, compared to randomly generated sightings.

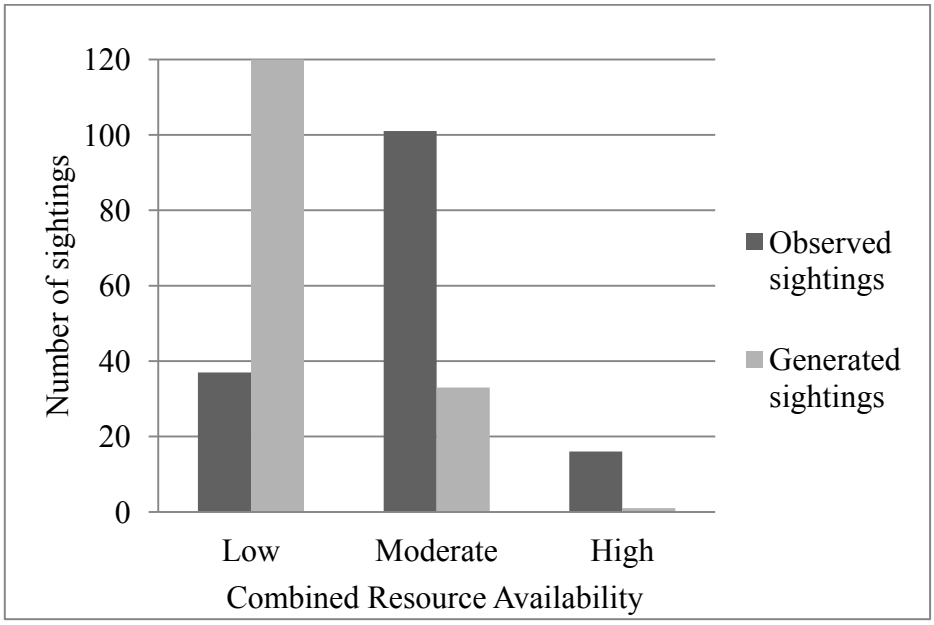

Figure 12: Association of observed sightings with three categories of the Combined Resource Availability Index, compared to randomly generated sightings.

Table 5: Summary of spatial analysis results.

RESOURCE INDEX	RESOURCE INDEX VALUE	SIGHTINGS VS. RANDOM (BINOMIAL Z SCORE)	PROBABILITY OF SIGHTINGS OBSERVED COMPARED TO EXPECTED BY CHANCE
Productivity (mg/m^3)			
	Low (< 0.3)	-5.88	Less
	Moderate (0.3-1)	2.61	More
	High (≥ 1)	4.46	More
Vulnerable Prey (km)			
	Low (≥50)	-5.90	Less
	Moderate (20–49.99)	1.47	Equal
	High (<20)	6.03	More
Combined Resource Availability			
	Low	-6.62	Less
	Moderate	5.87	More
	High	3.64	More

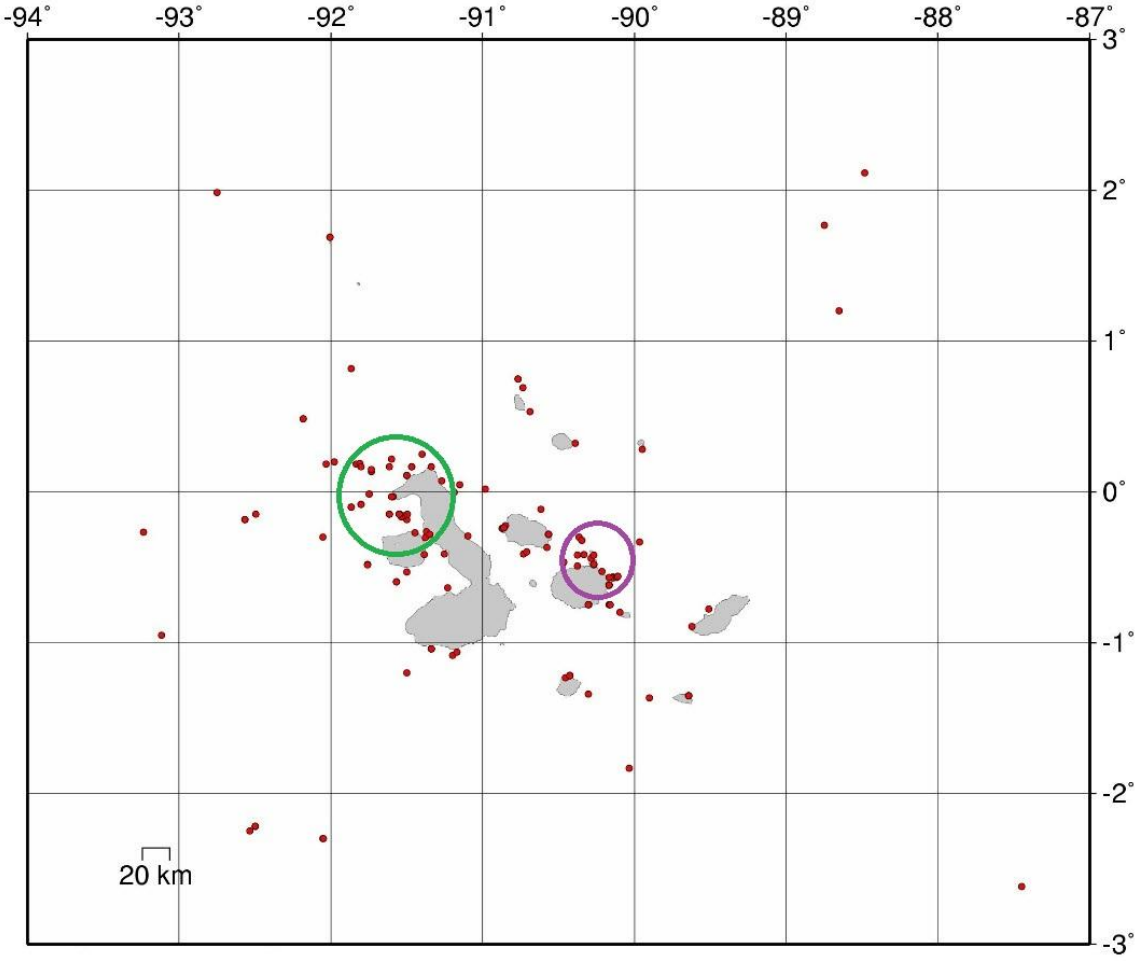

Figure 13: Killer whale sightings mapped with two areas of higher spatial use identified. The green circle encompasses northwest Isabela Island and the head of the Bolivar Canal; the purple circle encompasses Seymour Norte, Baltra, and northeast Santa Cruz.

Discussion

This is the first study to compile multiple data sets of killer whale sightings to test for a correlation between killer whale sightings and resource distribution in the GMR. Keeping in mind that research effort varied across time and space for the study period, these results can provide guidance for future research efforts and sharpen inductive reasoning about the habitat use of killer whales in the GMR.

Sightings were significantly correlated with the three resource variables tested: productivity, vulnerable prey, and combined resource availability. Autocorrelation between sea lion rookeries and higher chlorophyll a did not occur due to limited overlap in the two variables: sea lion rookeries mostly occur on the interior shores of the islands while higher levels of chlorophyll a occur on the exterior shores of the western-most islands. As a result most coastal areas of high chlorophyll a did not correspond to sea lion rookeries. Despite identifying a relationship between sightings and resource variables, how killer whales are using these resources, particularly areas with increased chlorophyll a, is still unknown. Within areas of high chlorophyll a concentrations, killer whales have been observed predating cetaceans, fish, sharks, and turtles. Unfortunately, little data are available on these resources with the exception of cetaceans, and the cetacean data are limited.

Though killer whale sightings were found to have a significant spatial correlation with sea lion rookeries, few direct observations of killer whales predating sea lions have been recorded. One predatory report recorded an individual half-beaching on a steep outcropping composed of boulders (Merlen, 1999), a behavior reminiscent of the feeding

tactic employed by the killer whales of Punta Norte, Argentina, and the Crozet Islands (Lopez and Lopez, 1985; Guinet, 1992; Hoelzel, 1991). Sea lion rookeries in the GMR are often in very shallow water and protected by volcanic rock outcroppings, which may be an anti-predator strategy by sea lions to avoid beach-based predation events (Alava, personal communication, 2011; personal observation, 2011). Adult GMR sea lions, both male and female, have been observed at least 100 kilometers from shore (personal observation); if sea lions routinely travel this far from shore, then some killer whales may have learned to predate them in open water rather than in the shallow coastal zone.

Conversely, the low number of reports of killer whales predating sea lions may be an indicator that sea lions do not play a significant role in the diet of GMR killer whales. There exists the possibility that the correlation between sightings and sea lion rookeries is actually an indicator of habitat quality, and killer whales and sea lions are both feeding in areas that exhibit a desirable quality, such as an abundance of fish or cephalopods. Killer whale foraging observations around northeast Santa Cruz, an area identified in this study with a greater concentration of sea lion rookeries (Figure 9) and killer whale sightings (Figure 13), are often of killer whales feeding on manta and eagle rays (Merlen, personal communication 2011).

This study provides insight into the distribution and resource association of GMR killer whales, but targeted research needs to be conducted to better understand the diet of killer whales in the GMR. Killer whales have been observed predating a diverse array of resources, which may be an indicator of the residency patterns of GMR killer whales. If killer whales in the GMR are comprised of different groups using the region throughout

the year, then the discrepancy in prey choice could be a result of the diet specialization of these diverse groups. If GMR killer whales are found to be composed of multiple sympatric ecotypes, like those along the Pacific coast of North America, this may result in distinct prey specializations (Ford et al, 1998). Finally, killer whales in the GMR may be unspecialized opportunistic predators, such as those found in the Crozet Islands and around Hawaii (Guinet, 1992; Baird et al, 2006).

Directed research efforts in the two areas circled in Figure 13 as having a greater abundance of sightings may yield more insight into foraging behavior and social structure. Additionally, as more research is conducted on the abundance and distribution of green sea turtles and fish in the GMR, an association between the distribution of these potential resources and killer whale sightings may be found. Further research needs to be conducted to determine if the spatial distribution of sightings within the GMR changes on a temporal basis. In Chapter IV, the results of Chapters II and III will be combined to test for a shift in the association between sightings and resource availability from the non-upwelling to upwelling season.

CHAPTER IV

TEMPORAL AND SPATIAL INTERACTION

Introduction

Spatial and temporal environmental factors are known to influence the distribution and habitat use of animals in both marine and terrestrial environments. Factors such as the photic period, temperature, and primary productivity can all influence when and where animals are distributed throughout their environment (e. g. Weir, 2007; Spyrakos, et al, 2011; Wal, et al, 2011). The seasonal abundance of resources in marine environments varies greatly between different latitudes and is influenced by both the duration of the photic period and the amount of free nutrients available (Racault et al, 2012).

In the arctic and sub-arctic waters the photic period changes drastically between seasons, with the sun being present nearly 24 hours/day during the summer and absent nearly 24 hours/day during the winter (Sewell and Jury, 2011; Teschke et al, 2011). The abundance of nutrients increases in the winter when phytoplankton is largely absent, generating an intense spring and summer bloom when the photic period is long and the water temperature increases (Sewell and Jury, 2011; Teschke et al, 2011). This results in short-growing high-amplitude phytoplankton and zooplankton blooms that comprise the basis of the food-web (Sewell and Jury, 2011; Teschke et al, 2011). Conversely, in the tropics and sub-tropics the photic period remains fairly constant throughout much of the year and the availability of nutrients act as the limiting factor in resource abundance

(Sewell and Jury, 2011; Teschke et al, 2011; Racault et al, 2012). In these regions blooms are generally characterized as long-growing with low-amplitude (Racault et al, 2012). Along coastal zones blooms may be more intense due to the forcing of nutrients to surface through upwelling, but in open-ocean pelagic ecosystems nutrients remain submerged below the level at which they can be utilized by phytoplankton (Sewell and Jury, 2011; Teschke et al, 2011; Racault et al, 2012).

The Galápagos Marine Reserve is a tropical marine environment with greater than average primary productivity due to seasonal upwelling and long photic periods (Palacios, 2004), Sweet et al, 2007; Schaeffer et al, 2008). Increased chlorophyll a levels enable increased levels of lower trophic level organisms, which in turn increase the abundance of mid-level trophic organisms (Hunt, 2006; Alava, 2009). Many of the prey items GMR killer whales have been observed predating are mid-level trophic organisms (e. g. fish, cephalopods, rays) (Alava, 2009). GMR killer whale sightings are known to be spatially associated with areas of high chlorophyll a concentrations and sea lion rookeries, however little is known about their diet or how that diet may change temporally (Merlen, 1999, Chapter III). Seasonal patterns of chlorophyll a concentrations could be a driving factor if GMR killer whale sightings are found to spatially shift with respect to temporal variability.

Killer whales have also been observed predating sea lions, a mobile upper level trophic organism, and the results of Chapter III indicate that the sighting distribution of killer whales is correlated with sea lions. Due to a lack of strong photoperiodic change, Galápagos sea lions do not exhibit the seasonal breeding synchrony common among

pinnipeds, and thus produce offspring year round (Villegas-Amtmann et al, 2009). If killer whales are foraging on resources influenced by seasonal upwelling, then they may prey switch to feed on sea lions when primary productivity decreases, resulting in a shift in the spatial distribution of sightings.

Although killer whales in the GMR have been observed predating a wide range of resources, from cetaceans to sea turtles, but it is unknown if there is dietary specialization within groups or social units (Merlen, 1999; Palacios, 2003, Alava and Merlen, 2009; Merlen, personal communication 2011). If GMR killer whales are specialized foragers then they may shift their distribution to follow their prey, or prey-shift between one or two important resources with different spatial distributions. If they are generalist predators, then there may be no significant shift in spatial distribution.

The aim of this chapter is to build on the results of Chapters II and III to gain a better understanding of how spatial sighting distribution may be influenced by temporal variability. To achieve this, I analyzed 20 years of data involving temporal and spatial distribution collected via ship-board line-transect surveys and observations of opportunity by an observer network.

Methods

Data collection and reduction

The data evaluated in this chapter are the same evaluated in Chapters II and III. Refer to Chapter II Methods for information on the data collection and reduction methods employed.

Data analysis

To assess whether the spatial distribution of killer whale sightings changed temporally, I tested for a relationship between each killer whale sighting per season (non-upwelling and upwelling) and the a) distance to the nearest sea lion rookery in kilometers, b) chlorophyll a level, and c) combination of distance to sea lion rookery and chlorophyll a level. I accessed chlorophyll a data through the Giovanni Online Data System, developed and maintained by the NASA Goddard Earth Sciences Data and Information Services Center and created a chlorophyll a map from MODIS 4km satellite data for each month of 2004 (GES-DISC, 2011). Because remotely sensed chlorophyll a data from the GMR were not routinely collected during the study period, I selected a year for analysis with available satellite coverage that exhibited no strong El Niño or La Niña trends. ArcGIS was used to map sea lion rookery data and the ArcGIS measuring tool to measure the distance in kilometers from each sighting to the nearest sea lion rookery. I then measured the level of chlorophyll a at each sighting for each corresponding month, such that if a sighting was recorded for January for any year of the study period, I mapped it on the January 2004 chlorophyll a map.

Sightings were assigned to a Productivity, Vulnerable Prey, and Combined Resource Availability Index as described in Chapter III (see Chapter III Methods and Table 3). The Productivity Index measured the level of chlorophyll a present at each sighting and the Vulnerable Prey Index measured the distance in kilometers from each sighting to the nearest sea lion rookery. The Combined Resource Availability Index value for each sighting was generated by combining the values from the Productivity and Vulnerable Prey Indices. I used a binomial z test (Bakeman and Gottman, 1986) to compare the probability of co-occurrence of killer whale sightings per season for each resource category. Because the number of sightings each season are not equal, I measured whether the probability of sightings in the upwelling season occurred more than, less than, or equal to the probability of sightings observed in the non-upwelling season.

Results

Upwelling and non-upwelling sightings were observed with equal probability for all three levels of the Productivity Index: high (binomial $z = -0.05$, $p>0.05$); moderate (binomial $z = -0.27$, $p>0.05$); low (binomial $z = 0.58$, $p>0.05$) (Figure 14, Table 6). Sightings between the two seasons were also found to occur with equal probability for all three categories of the Vulnerable Prey Index: high (binomial $z = 1.54$, $p>0.05$); moderate (binomial $z = -0.77$, $p>0.05$); and low (binomial $z = -1.60$, $p>0.05$) (Figure 15, Table 6). However, there was a difference in the occurrence of upwelling sightings compared to non-upwelling sightings for the Combined Resource Availability Index. Upwelling sightings were observed with equal probability for the high (binomial $z = 0.56$, $p>0.05$) and moderate (binomial $z = 1.73$, $p>0.05$) resource levels and less often than expected for the low level (binomial $z = -3.17$, $p<0.05$) (Figure 16, Table 6). The spatial mapping of sightings in the non-upwelling (Figure 17) and upwelling (Figure 18) seasons provided a clear visualization of the decrease in sightings in areas of low resource value during the upwelling season compared to the non-upwelling season. Sightings in the non-upwelling season were more scattered within the study area and sightings were more clustered in areas of increased combined resource productivity for the upwelling season.

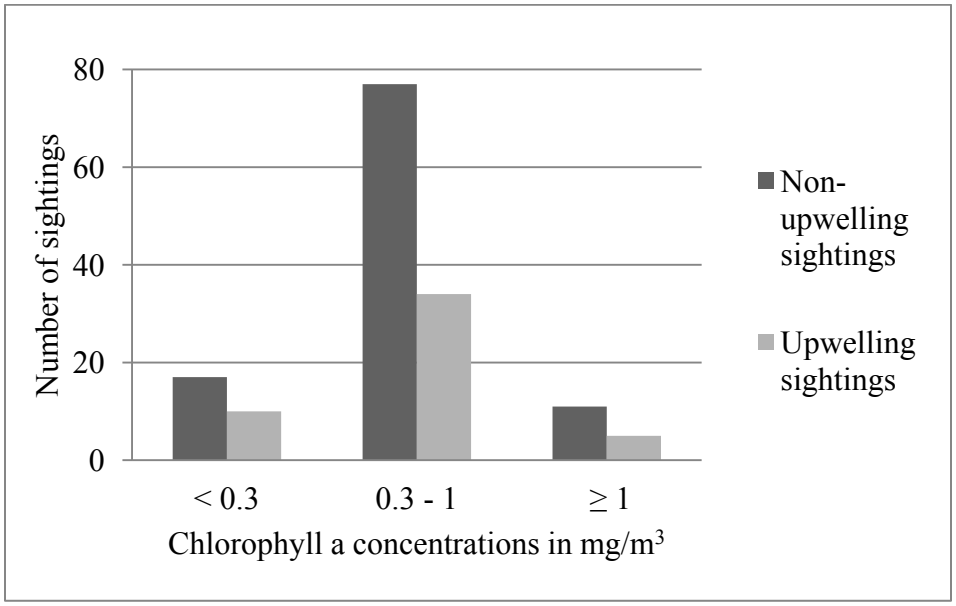

Figure 14: Non-upwelling versus upwelling sightings per level of the Productivity Index.

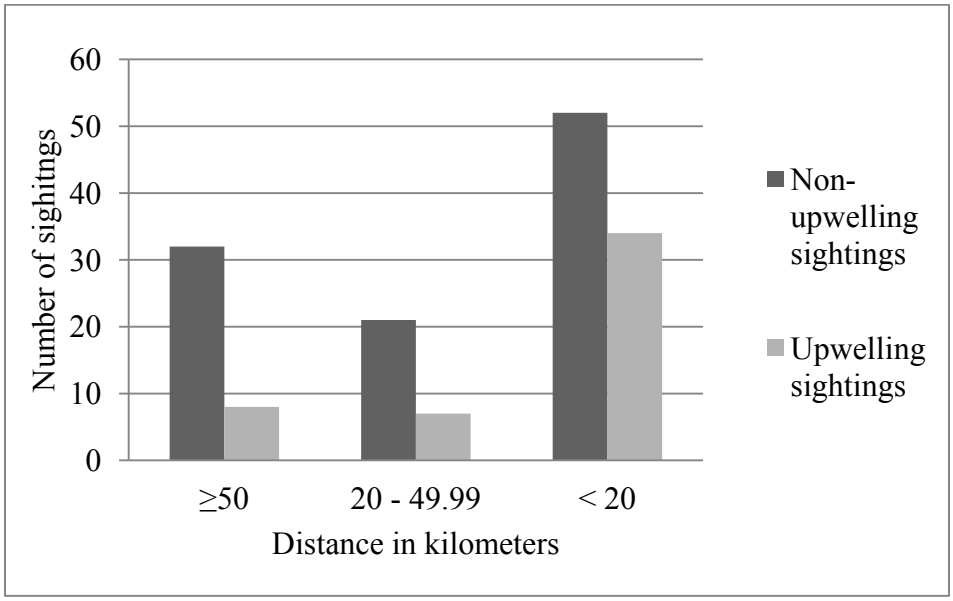

Figure 15: Non-upwelling versus upwelling sightings per level of the Vulnerable Prey Index.

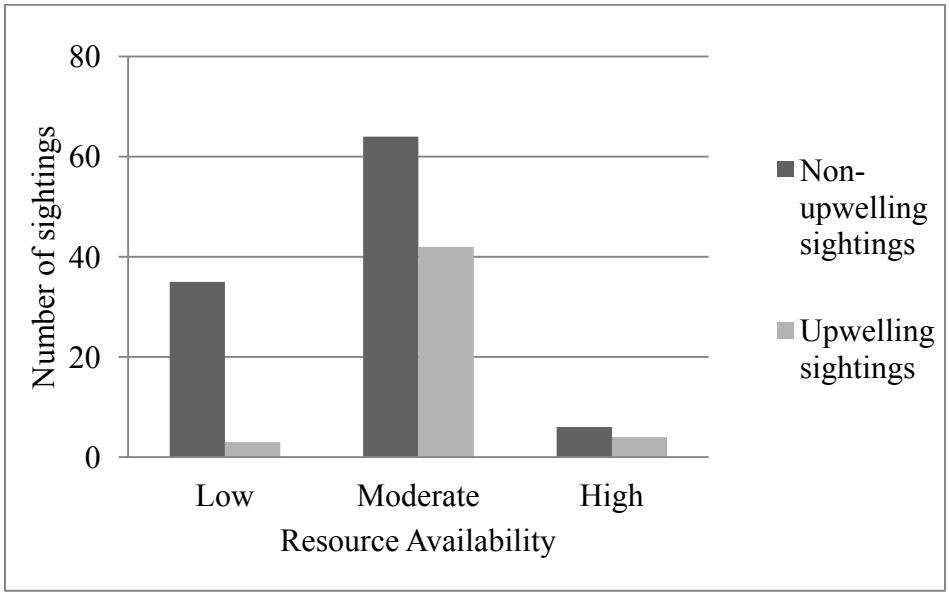

Figure 16: Non-upwelling versus upwelling sightings per level of the Combined Resource Availability Index.

Table 6: Summary of temporal-spatial analysis results

RESOURCE INDEX	RESOURCE INDEX VALUE	UPWELLING VS NON-UPWELLING SIGHTINGS (BINOMIAL Z SCORE)	PROBABILITY OF UPWELLING SIHTINGS VS NON-UPWELLING SIGHTINGS
Productivity (mg/m^3)			
	Low (< 0.3)	0.58	Equal
	Moderate (0.3-1)	-0.27	Equal
	High (≥ 1)	-0.05	Equal
Vulnerable Prey (km)			
	Low (≥50)	-1.6	Equal
	Moderate (20–49.99)	-0.77	Equal
	High (<20)	1.54	Equal
Combined Resource Availability			
	Low	-3.17	Less
	Moderate	1.73	Equal
	High	0.56	Equal

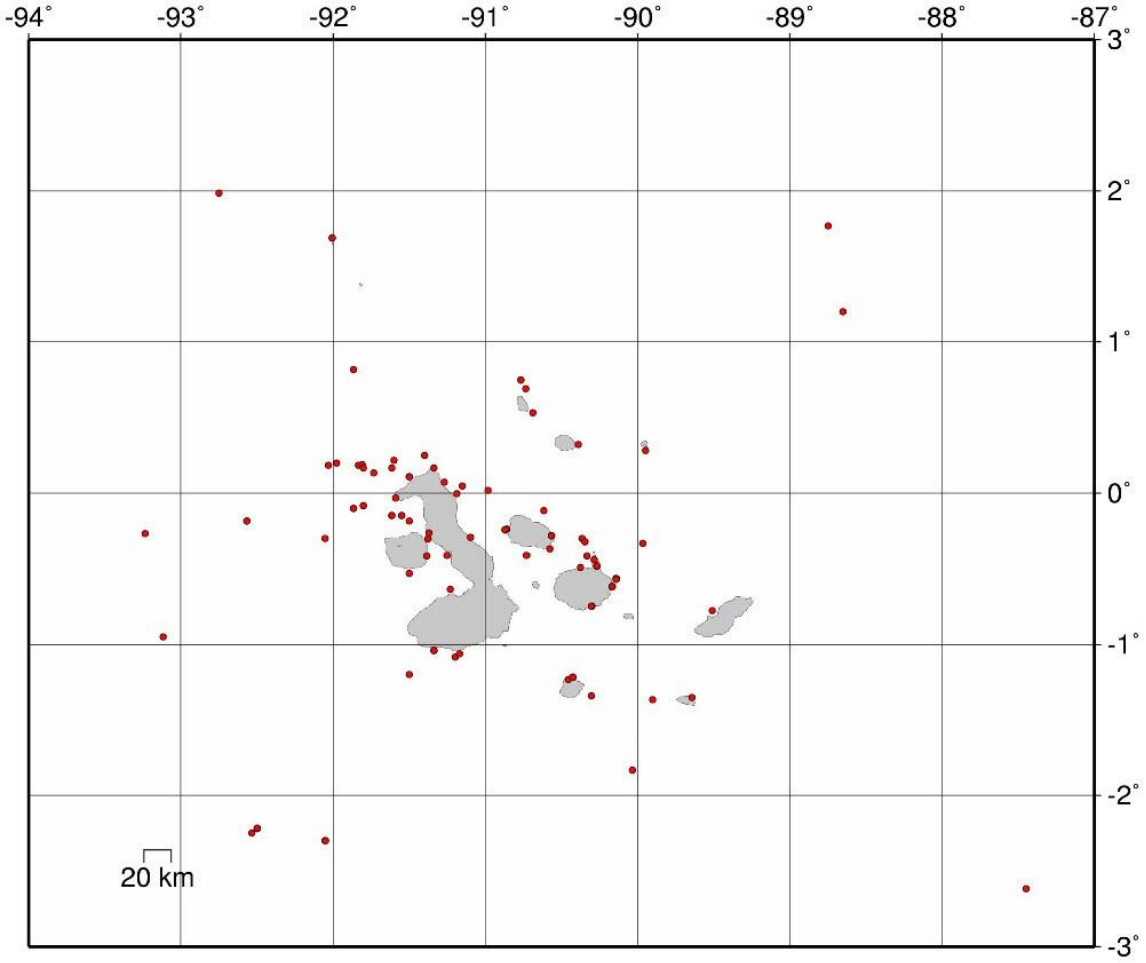

Figure 17: Spatial distribution of sightings during the non-upwelling season.

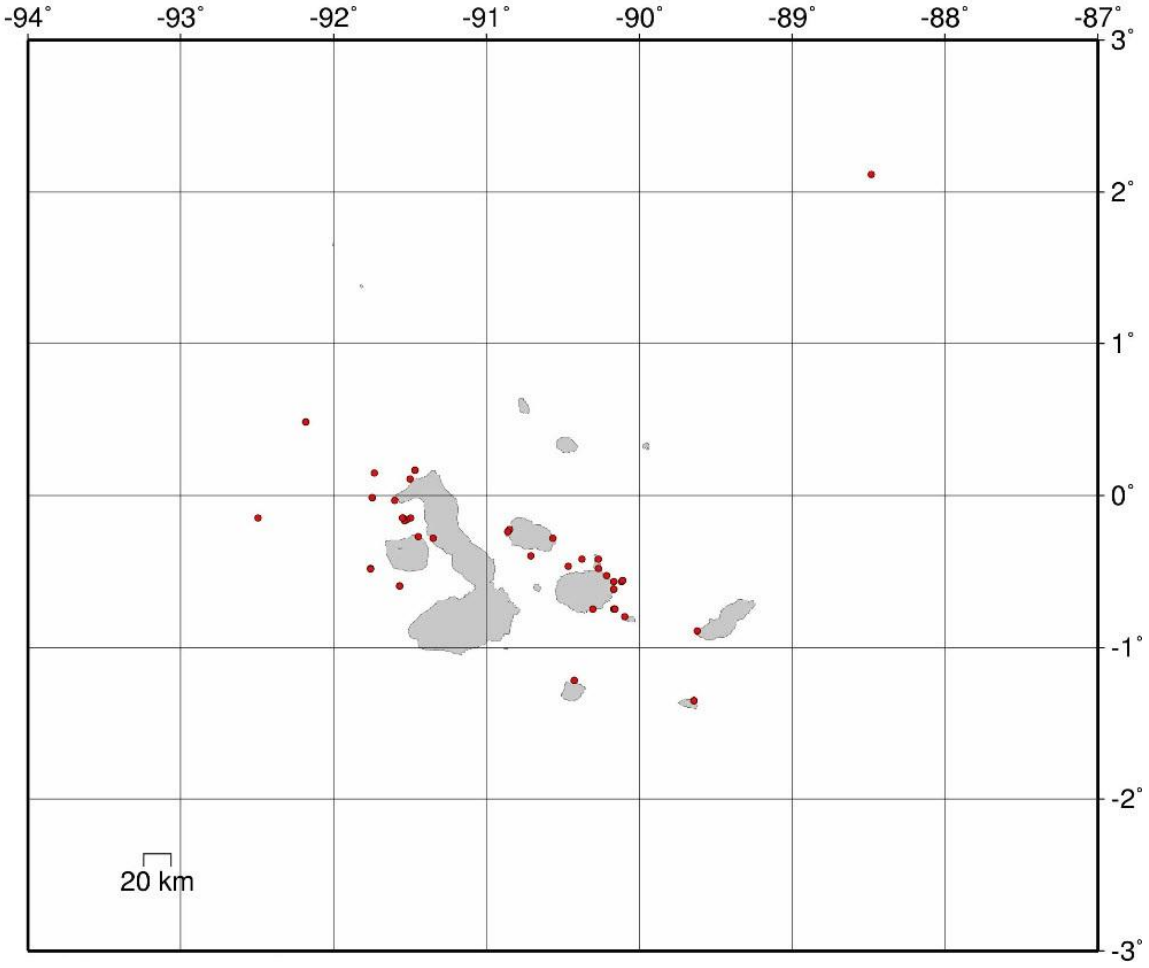

Figure 18: Spatial distribution of sightings during the upwelling season.

Discussion

This study builds on the temporal and spatial results from Chapters II and III, and is the first study to synthesize multiple sets of killer whale sightings in the GMR and test for a spatial shift in sightings with respect to temporal change. In Chapter II, I reported that killer whales are present in the GMR all year, with a slight increase in expected sightings in the peak upwelling period of August – November. In Chapter III, killer whale sightings were shown to be spatially associated with sea lion rookeries (Vulnerable Prey Index), areas of high chlorophyll a concentrations (Productivity Index), and areas with resource overlap (Combined Resource Availability Index). With the understanding that data collection methods varied in effort across time and space, the results of this study provide insight into the temporal and spatial habitat use of killer whales in the GMR.

Sighting distribution did not change between seasons with respect to the Productivity, Vulnerable Prey, or Combined Resource Availably Indices. However, during the peak upwelling period identified in Chapter II, killer whale sightings occurred less often than expected in areas of low productivity. It is uncertain why killer whale distribution changes for this variable, but it could be an indicator that important resources, such as migratory whales, may be clustering around areas of high productivity and thus influencing a shift in killer whale distribution.

These results indicate that killer whales are not making a significant prey switch (e. g. sea lions to fish) between seasons. This could be a result of year-round unspecialized foraging in areas of higher abundance, as hypothesized in Merlen (1999)

and Chapter III. If killer whales in the GMR are comprised of multiple populations passing through the region throughout the year, then physical drivers outside of the scope of this study may be driving killer whales to forage more heavily in areas of high resource abundance during upwelling.

This study demonstrates that killer whales sightings are spatially associated with resources, though there seems to be little temporal effect on that association. That sightings occurred less often in areas of low productivity during upwelling seasons is interesting, but more research needs to be conducted to better understand what this means regarding killer whale residency and behavioral ecology.

CHAPTER V

SUMMARY AND CONCLUSIONS

Summary

The goal of this study was to answer three basic questions about killer whales in the Galápagos Marine Reserve and surrounding waters: a) is there a temporal pattern to killer whale sightings; b) are sightings spatially associated with potential resources (chlorophyll a or sea lion rookeries); and c) if sightings are spatially associated with resources, does the spatial distribution of sightings change temporally? Sighting data were collected between 1976 and 1997 via shipboard line-transect survey and opportunistic sightings by an observer network (n = 154).

In Chapter II, I tested for a temporal pattern to killer whale sightings in three different ways: i) bi-seasonal variation, ii) inter-annual ENSO influence and iii) a combination of seasonal and ENSO event influence. I found that sightings occurred in every month of the year, though not every month every year, and were roughly equally distributed between the non-upwelling and upwelling seasons. The strength of ENSO events did not have a significant influence on the number of sightings from year to year. Sightings were found to occur more often than expected by chance in the peak upwelling series of August – October and August – November when the MEI was within one standard deviation of the norm.

In Chapter III, I tested for a spatial association between sightings and three resource variables: i) chlorophyll a concentrations (Productivity Index), ii) distance to

sea lion rookeries (Vulnerable Prey Index) and iii) the combined value of chlorophyll a and distance to sea lion rookeries (Combined Resource Availability Index). Sightings were found to occur more often than expected by chance when Productivity Index levels were high ($\geq$ 1mg/m^3) and moderate (0.3 – 0.99mg/m^3) and less often than expected by chance when Productivity Index levels were low (<0.3mg/m^3). Sightings occurred more often than expected by chance when <20km from sea lion rookeries, with equal occurrence of chance 20 – 49km from rookeries, and less than expected by chance ≥50km from rookeries. When these two resource variables were explored in more detail sightings were found to occur more often than expected in areas of high and moderate combined resource availability, and less often than expected in areas with low combined resource availability. Additionally, sightings were more concentrated in two areas: northwest Isabela Island and the head of the Bolivar Canal; and Seymour Norte, Baltra, and northwest Santa Cruz.

In Chapter IV, the results from Chapters II and III were used to test for a spatial change in sighting distribution with respect to temporal variability. Using the four month upwelling peak identified in Chapter II (August – November), I compared the number of sightings per level of resource category for each season. I found that the number of sightings for both seasons did not significantly shift for either the Productivity or Vulnerable Prey Indices. The number of sightings for high and moderate Combined Resource Availability Index levels did not change between seasons, but sightings were significantly less likely to occur in areas of low combined resource availability in the upwelling season.

Conclusions

The results of this study show killer whales are present in the Galápagos Marine Reserve throughout the year. In most years, killer whale presence does not appear to be influenced by El Niño Southern Oscillation Events. Sighting abundance did increase during the peak upwelling months when the MEI was normal, but this could be an artifact of increased boat activity and thus more opportunities to sight killer whales. Because resources are more abundant during times of increased productivity there may be more observers (e.g. fishermen, divers) on the water to use those resources, thus increasing the number of sightings. This is not conclusive but should be considered when interpreting these results. The residency patterns of GMR killer whales remain unsolved and require further research. That sightings were recorded every month is a strong indicator that the presence of killer whales in the GMR is not limited to times of high productivity or resource pulses. However, the residency patterns of killer whales are still unknown, and there may exist a single resident population, multiple resident and transient populations, or that killer whales observed in the GMR may be part of the ETP population and routinely visit the region.

The correlation between sightings and areas of primary productivity implies that killer whales are foraging in areas of increased productivity where mid-trophic level resources may be more abundant. Foraging observations of killer whales in these areas indicate they are predating rays, sharks, fish, and other cetaceans (Arnbom et al, 1987; Merlen, 1999; Palacios, 2003; Alava, 2009), which may be in the area due to the increased availability of prey resources. While sightings were found to be spatially

correlated with sea lion rookeries, it needs to be remembered that correlation does not equal causation. Reports of GMR killer whales attacking sea lions and fur seals have been documented, but not with any great abundance (Merlen, 1999; Merlen, personal communication 2010). There exists the possibility that killer whales and sea lions are sympatric populations utilizing the same areas due to a desirable habitat quality, such as an abundance of fish or cephalopod resources. If killer whales in the GMR are later found to be comprised of different ecotypes, there may well be an ecotype that predates sea lions and a type that does not. The greater number of sightings in northwest Isabela Island and the head of the Bolivar Canal, and Seymour Norte, Baltra, and northeast Santa Cruz each coincide with increased resource availability. The northwest Isabela/Bolivar Canal region is an area of increased upwelling and chlorophyll a concentrations, while the area of northeast Santa Cruz is the location of many sea lion rookeries.

When examining whether the spatial distribution of sightings may have a temporal component, I found significantly less sightings occurred in areas of low productivity in the upwelling season, when resources are likely most abundant. This may mean that if most killer whales in the GMR are transient or migratory they may be using the area more for foraging and less for travelling during these times. More research needs to be conducted to better understand how killer whales are using the GMR.

Recommendations for future research

While this study answers basic questions about killer whale presence in the Galápagos Marine Reserve and surrounding waters, future research is needed to gain a better understanding of their behavioral ecology. I identified two locations in the GMR (northwest Isabela Island and west Baltra/Seymour Norte) where killer whales are more frequently sighted, which may prove to be productive areas to base future research projects. Increased boat-based survey effort in both locations could yield important data on social interactions, predatory behavior, and provide opportunities to acquire skin sloughs and fecal matter for genetic and physiology studies. Photos of individuals could be used to generate a photo ID catalog to assist in identifying social units and provide more information about killer whale residency in the region. Stationary underwater acoustic devices could be used to monitor killer whale presence in an area and to collect vocalization data. Though more invasive, the use of satellite tags and biopsy darts could be effective tools to gain insight into killer whale movement patterns, diet, health, and genetics.

This study focused on the affects of bottom-up influences on killer whales (e. g. resource distribution), but future studies focused on the top-down influence of killer whales on the environment could be useful. Examples of this include comparing the behavior and feeding tactics of sea lions within killer whale “hot spots” and those from other locations, or monitoring changes to migrant whale behavior when in the vicinity of killer whales or in areas where killer whales are more frequently observed. These types of studies may provide additional clues to killer whale foraging and resource use.

REFERENCES

ALAVA, J. J. (2009) Carbon productivity and flux in the marine ecosystems of the Galápagos Marine Reserves based on cetacean abundances and trophic indices. *Revista de Biologia Marina y Oceanografia* 44(1): 109 – 122.

ALAVA, J.J. AND MERLEN, G. (2009) Video-documentation of a killer whale (*Orcinus orca*) predatory attack on a giant manta (*Manta birostris*) in the Galápagos Islands. *Latin American Journal of Aquatic Mammals* **7**(1-2): 81-84.

ALAVA, J. J. AND SALAZAR, S. (2006) Status and Conservation of Otariids in Ecuador and the Galápagos Islands. Pages 495 – 519 *in* TRITES, A. W., ATKINSON, S. K., DEMASTER, D. P, FRITZ, L. W., GELATT, T. S., REA, L. D., AND WYNNE, K. M. (Eds) *Sea Lions of the World* Alaska Sea Grant College Program, University of Alaska Fairbanks. Fairbanks, Alaska, USA**.**

ANDREWS, R. D., PITMAN, R. L., AND BALLANCE, L. T. (2008) Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biology* 31: 1461 – 1468.

ARNBOM, T., PAPASTAVROU, V., WEILGART, L. S., AND WHITEHEAD, H. (1987) Sperm whales react to an attack by killer whales. *Journal of Mammalogy* 68(2): 450 – 453.

BAIRD, R. W., MCSWEENEY, D. J., BANE, C., BARLOW, J., SALDEN, D. R., ANTOINE, L. K., LEDUC, R. G., AND WEBSTER, D. L. (2006) Killer whales in Hawaiian waters: information on population identity and feeding habits. *Pacific Science* 60(4): 523- 530.

BAKEMAN, R. AND GOTTMAN, J.M. (1986) Observing interaction: an introduction to sequential analysis. Cambridge: Cambridge University Press. p. 118-168.

BALLANCE, L. T., PITMAN, R. L. AND FIEDLER, P. C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in Oceanography* 69(2-4): 360-390.

BARRETT-LENNARD, L. G., MATKIN, C. O., DURBAN, J. W., SAULITIS, E. L., AND ELLIFRIT, D. (2011) Predation on gray whales and prolonged feeding on submerged carcasses by transient killer whales at Unimak Island, Alaska. *Marine Ecology Progress Series* 421: 221-241.

BENSON, S. R., CROLL, D. A., MARINOVIC, B. B., CHAVEZ, F. P., AND HARVEY, J. T. (2002) Changes in the cetacean assemblages of a coastal upwelling ecosystem during El Niño 1997 – 1998 and La Niña 1999. *Progress in Oceanography* 54: 279 – 291.

DAHLHEIM, M. E. (1997) A Photographic Catalog of Killer Whales, *Orcinus orca*, from the Central Gulf of Alaska to the Southeastern Bering Sea. NOAA Technical Reports NMFS 131.

DAHLHEIM, M. E., SCHULMAN-JANIGER, A., BLACK, N., TERNULIO, R., ELLIFRIT, D., AND BALCOMB, K. C. (2008). Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): Occurrence, movement, and insights into feeding. *Marine Mammal Science* 24(3): 719 – 729.

DURBAN, J., ELLIFRIT, D., DAHLHEIM, M., WAITE, J., MATKIN, C., BARRETT-LENNARD, L., ELLIS, G., PITMAN, R., LEDUC, R., AND WADE, P. (2010) Photographic mark-recapture analysis of clustered mammal-eating killer whales around the Aleutian Islands and Gulf of Alaska. *Marine Biology* 154: 1591-1604.

DURBAN, J.W. AND PITMAN, R. L. (2011) Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological; maintenance migrations? *Biology Letters* doi: 10.1098/rsbl.2011.0875

EDGAR, G.J., BANKS, S.A., BRANDT, M., BUSTAMANTE, R. H., CHIRIBOGA, A., EARLE, S. A., GARSKE, L. E., GLYNN, P. W., GROVE, J. S., HENDERSON, S., HICKMAN, C. P., MILLER, K. A., RIVERA, F., AND WELLINGTON, G. M. (2010) El Niño, grazers, and fisheries interact to greatly elevate extinction risk for Galápagos marine species. *Global Change Biology* 16: 2876-2890

ESRI (2011). Available at <http://arcscripts.esri.com/details.asp?dbid=12098> Consulted 3 March, 2011)

ESRL (2011). Earth Systems Research Laboratory. Available online at <http://www.esrl.noaa.gov/psd/enso/mei/table.html> Consulted 19 February 2011.

FARIÑA, J. M., SALAZAR, S., WALLEM, P., WITMAN, J. AND ELLIS, J. S. (2003) Nutrient exchanges between marine and terrestrial ecosystems: the case of the Galápagos sea lion (*Zalophus wollebaeki*). *Journal of Animal Ecology* 72:873–887.

FLORES-RAMIREZ, S., URBAN, J., VILLAREAL-CHAVEZ, G., AND VALLES-JIMENEZ, R. (1996) Spatial and temporal changes in the cetacean community structure at Bahia de la Paz, B.C.S., Mexico (1988-1991). *Ciencias Marinas* 22(2): 151 – 173.

FOOTE, A. D., SIMILA, T., VIKINGSSON, G. A., STEVICK, P. T. (2010) Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolution and Ecology* 24: 803 – 814.

FORD, J. K. B., ELLIS, G. M., BARRETT-LENNARD, L. G., MORTON, A. B., PALM, R. S., AND BALCOMB, K. C. (1998) Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76(8): 1456 – 1471.

GARDNER, S. C. AND CHAVEZ-ROSALES, S. (2000) Changes in the relative abundance and distribution of gray whales (*Eschrichtius robustus*) in Magdelena Bay, Mexico during an El Niño event. *Marine Mammal Science* **16**(4): 728 – 738.

GES-DISC (2011). Goddard Earth Sciences Data and Information Services Center Interactive Online Visualization and Analysis Infrastructure. Available at <http://disc.sci.gsfc.nasa.gov/giovanni#maincontent> Consulted 19 February, 2011; 26 March, 2011.

HAUSER, D. D. W., LOGSDON, M. G., HOLMES, E. E., VANBLARICOMB, G. R., AND OSBORNE, R. W. (2007) Summer distribution patterns of southern resident killer whales *Orcinus orca*: core areas and spatial segregation of social groups. *Marine Ecology Progress Series* 351: 301 – 310.

GUINET, C. (1992) Comportement de chasse des orques (*Orcinus orca*) autour des iles Crozet. *Canadian Journal of Zoology* 70(9): 1656 – 1667.

GUINET C., BARRETT-LENNARD L. G., LOYER B. (2000) Co-ordinated attack behavior and prey sharing by killer whales at Crozet Archipelago: strategies for feeding on negatively-buoyant prey. *Marine Mammal Science* 16: 829–834.

HOELZEL, A. R. (1991) Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning, and foraging strategy. *Behavioral Ecology and Sociobiology* 29: 197- 204.

HUNT, G. L. (2006) Evidence for bottom-up control of upper-trophic-level marine populations. Pages 50-64 *in* ESTES, J.A., DEMASTER, D.P., DOAK, D. F., WILLIAMS, T.M., AND BROWNELL, R. L. (Eds) *Whales, Whaling, and Ocean Ecosystems.* University of California Press. Berkeley and Los Angeles California, USA.

JEGLINSKI, J. W. E, WERNER, C., GOETZ, K. T., COSTA, D. P., AND TRILLMICH, F. (2011) Niche competition: do juvenile Galápagos sea lions compete with adult Galápagos fur seals? 19th Biennial Conference on the Biology of Marine Mammals. Tampa, Florida, USA. November 28 – December 3, 2011.

KARNAUSKAS, K.B., MURTUGUDDE, R., AND BUSALACCHI, A.J. (2010) Observing the Galápagos-EUC interaction: insights and challenges. *Journal of Physical Oceanography* 40: 2768-2777.

KRAHN, M. M., HERMAN, D. P., MATKIN, C. O., DURBAN, J. W., BARRETT-LENNARD, L., BURROWS, D. G., DAHLHEIM, M. E., BLACK, N., LEDUC, R. G., AND WADE, P. R. (2007) Use of chemical tracers in assessing the diet of foraging regions of eastern North Pacific killer whales. *Marine Environmental Research* 63: 91 – 114.

LOPEZ, J. C. AND LOPEZ, D. (1985) Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. *Journal of Mammalogy* 66(1): 181 – 183.

MATKIN C. O., BARRETT-LENNARD L. G., YURK H, ELLIFRIT D. K., TRITES A. W. (2007) Ecotypic variation and predatory behavior of killer whales (*Orcinus orca*) in the eastern Aleutian Islands, Alaska. *Fish Bulletin* 105:74–87.

MATTHEWS, C. J. D., LUQUE, S. P., PETERSON, S. D., ANDREWS, R., D., FERGUSON, S. H. (2011) Satellite tracking of a killer whale (*Orcinus orca*) in the eastern Canadian Arctic documents ice avoidance and rapid, long-distance movement to the North Atlantic. *Polar Biology* 34: 1091 – 1096.

MERLEN, G. (1999) The orca in the Galápagos: 135 sightings. *Noticias de Galápagos* 60: 2-8.

MERLEN, G. (2000) Nocturnal acoustic locations of the Galápagos fur seal *Arctocephalus galapagoensis*. *Marine Mammal Science* 16(1): 248 – 253.

OLSON, P. A. AND GERRODETTE, T. (2008) Killer Whales of the Eastern Tropical Pacific: A Catalog of Photo-Identified Individuals. NOAA Technical Memorandum NMS-SWFSC-428.

PALACIOS, D.M. (2003) Oceanographic conditions around the Galápagos Archipelago and their influence on cetacean community structure. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon. 178 pp.

PALACIOS, D. M. (2004) Seasonal patterns of sea-surface temperatures and ocean color around the Galápagos: regional and local influences. *Deep Sea Research II* 51: 43 – 57.

PISTORIUS, P. A., TAYLOR, F. E., LOUW, C., HANISE, B., BESTER, M. N., DE WET, C., DU PLOOY, A., GREEN, N., KLASEN, S., PODILE, S., AND SCHOEMAN (2002) Distribution, movement, and estimated population size of killer whales at Marion Island, December 2000. *South African Journal of Wildlife Research* 32(1): 86 – 92.

RACAULT, M. F., LA QUERE, C., BUITENHUIS, E., SATHYENDRANATH, S., AND PLATT, T. (2012) Phytoplankton phenology in the global ocean. *Ecological Indicators* 14(1): 152-163

REISINGER, R. R., DE BRUYN, P. J. N., TOSH, C. A., OOSTHUIZEN, W. C., MUFANADZO, N. T., AND BESTER, M. N. (2011) Prey and seasonal abundance of killer whales at sub-Antarctic Marion Island. *African Journal of Marine Science* 33(1): 99 – 105.

SALVADEO, C. J., FLORES-RAMIREZ, S., GOMEZ-GALLARDO, A., MACLEOD, U., LLUCH-BELDA, D., JUAME-SCHINKEL, S. AND URBAN, J. (2011) Bryde's whale (*Balaenoptera edeni*) in the southwestern Gulf of California: Relationship with ENSO variability and prey availability. *Ciencias Marinas* 37(2): 215 – 225.

SCHAEFFER, B.A., MORRISON, J.M., KAMYKOWSKI, D., FELDMAN, G. C., XIE, L., SWEET, W., MCCULLOCK, A., AND BANKS, S. (2008) Phytoplankton biomass distribution and identification of productive habitats within the Galápagos Marine Reserve by MODIS, a surface acquisition system, and *in situ* measurements. *Remote Sensing of Environment* 112: 3044-3054

SEWELL, M. A. AND J. A. JURY. (2011) Seasonal patterns in diversity and abundance of the High Antarctic meroplankton: Plankton sampling using a Ross Sea desalination plant. *Limnology and Oceanography* 56(5): 1667-1681.

SMITH, S. C. AND WHITEHEAD, H. (1993) Variations in the feeding success and behavior of Galápagos sperm whales (*Physeter-macrocephalus*) as they relate to oceanographic conditions. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 71(10): 1991-1996.

SORISIO, L. S., DE MADDALENA, A., AND VISSER, I. N. (2006) Interaction between killer whales (*Orcinus orca*) and hammerhead sharks (*Sphyrna* sp.) in Galápagos waters. *Latin American Journal of Aquatic Mammals* 5(1): 69 -71

SPYRAKOS, E., SANTOS-DINIZ, T. C., MARTINEZ-IGLESIAS, G., TORRES-PALENZUELA, J. M., AND PIERCE, G. J. (2011) Spatiotemporal patterns in marine mammal distribution in coastal waters of Galicia, Spain. *Hydrobiologia* 670: 87 – 109.

SWEET, W.V., MORRISON, J.M., KAMYKOWSKI, D., SCHAEFFER, B. A., BANKS, S., AND MCCULLOCH, A. (2007) Water mass seasonal variability in the Galápagos Archipelago. *Deep-Sea Research* I 54: 2023-2035

TESCHKE, M., WENDT, S, KAWAGUCHI, S., KRAMER, A, AND MEYER, B. (2011) A circadian clock in Antarctic krill: an endogenous timing system governs metabolic output rhythms in the euphausid species *Euphausia superb***.** *PLoS One* 6(10): DOI: 10.1371/journal.pone.0026090

TRILLMICH, F. AND LIMBERGER, D. (1985) Drastic effects of El Niño on Galápagos Pinnipeds. *Oecologia* 67(1): 19-22.

VARGAS, F. H., LACY, R. C., JOHNSON, P. J., STEINFURTH, A., CRAWFORD, R. J. M., BOERSMA, P. D., AND MACDONALD, D. W. (2007) Modeling the effect of El Niño on the persistence of small populations: The Galápagos penguin as a case study. *Biological Conservation* 137(1): 138-148.

VILLEGAS-AMTMANN, S., ATKINSON, S, AND COSTA, D. P. (2009) Low synchrony in the breeding cycle of Galápagos sea lions revealed by seasonal progesterone concentrations. *Journal of Mammalogy* 90(5): 1232 – 1237.

WADE, P. R. AND GERRODETTE, T. (1993) Estimates of Cetacean Abundance and Distribution in the Eastern Tropical Pacific. *Reports of the International Whaling Commission* 43:477 – 494.

WAL, E. V., MCLOUGHLIN, P. D., AND BROOK, R. K. (2011) Spatial and temporal factors influencing sightability of elk. *The Journal of Wildlife Management* 75(6): 1521 – 1526.

WEIR, C. R., STOCKIN, K. A., AND PIERCE, G. J. (2007) Spatial and temporal trends in the distribution of harbor porpoises, white-beaked dolphins and minke whales off Aberdeenshire (UK), north-western North Sea. *Journal of the Marine Biology Association of the UK* 87: 327 – 338.

VITA

Kerri Jean Smith received her Bachelor of Science degree in marine biology from Texas A&M University at Galveston in 2008. She entered the Marine Biology Interdisciplinary Program at Texas A&M in August 2009 and will receive the Master of Science degree in May 2012. She is broadly interested in the behavioral ecology and ecophysiology of marine predators, particularly marine mammals, seabirds and sharks; the complex nature of marine ecosystems; and marine biodiversity and conservation. She plans to pursue a PhD and continue marine ecosystem research.

Ms. Smith can be reached by e-mail to SmithKerriJ@gmail.com and mail to 2258 TAMU, College Station, TX 77843.